A taxonomic revision of the southern Arabian Enidae *sensu lato* (Mollusca; Pulmonata)

Peter B. Mordan

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Introduction

Although characterised by relatively low levels of faunal diversity, the Arabian peninsula occupies an important geographic position at the boundary of three of the world's major biogeographic zones—the Palaearctic, Afrotropical, and Oriental. It is a region of taxonomic and biogeographic discontinuity, not only for land molluscs (Mordan, 1980b) but also for many other taxa. Whilst land snails show remarkable distributional stability through time (Solem, 1979), and thus represent a highly suitable group for biogeographic analysis, the value of their contribution to many such studies has been limited by the inadequacy of our knowledge of their taxonomy (Peake, 1978).

The non-marine Mollusca of southern Arabia, an area defined here broadly as that part of the peninsula south to the Tropic of Cancer but including the whole of Oman, were last comprehensively reviewed by Connolly (1941). To the end of this paper Connolly appended a list of 164 species of land and freshwater Mollusca from the region, with the pertinent comment that, of those species whose distribution is restricted to southern Arabia, 'half the names are probably superfluous and should be relegated to synonymy' (Connolly, 1941:40). Although a small number of junior synonyms were included, the list remained essentially uncritical. Subsequently a

series of regional reviews has appeared covering South Yemen and Dhofar (Fischer-Piette & Métivier, 1972), North Yemen (Verdcourt, 1974), Saudi Arabia (Mordan, 1980a), and Oman (Smythe & Gallagher, 1977; Mordan, 1980b), but all are based essentially on conchological material.

Members of the family Enidae s.l. consitute by far the most numerous single element in the southern Arabian land-snail fauna, accounting for well over one-third of the total number of terrestrial species listed by Connolly. In an earlier paper (Mordan, 1984) the status of subfamily units within the Enidae was considered, with especial reference to the Arabian fauna, and the anatomical differences between the groups summarised. On the basis of these differences, particularly of the reproductive and pallial systems, two major groupings were recognised: the northern Enidae s.s. comprising the subfamilies Chondrulinae and Eninae, as defined by Forcart (1940); and the southern Cerastinae sensu Zilch (1959). These two groups have broadly non-overlapping ranges, but both are represented in southern Arabia. From the analysis it was also concluded that there was no evidence for the two being sister groups in a cladistic sense, and thus the Enidae s.l. could not be considered a monophyletic taxon. Formalising the status of the Cerastinae has, however, been deferred until there is a greater knowledge of the related orthurethran families, and consequently the present paper retains all three subfamilies within the Enidae s.l.. The biogeographic implications of these conclusions were considered in some detail in the earlier paper and will not be repeated here. The name Cerastinae Wenz, 1923 is used as it has priority over Pachnodinae Steenberg, 1925, and has the type genus Cerastus Albers, 1860; Cerastus Dejean, 1821 must be considered a nomen nudum under Article 12 of the International Code of Zoological Nomenclature.

The present paper is a review of the taxonomy of the Arabian enids using the admittedly incomplete anatomical information available. Whilst it is primarily concerned with genus- and species-level distinction, the opportunity is taken to discuss, in greater detail than was possible in the earlier paper, the anatomical characters relevant to the higher-level taxonomy of the Enidae as exemplified by the Arabian forms. No analysis of phylogeny has been attempted as this will form the subject of a further paper reviewing all cerastine genera.

The work is based primarily on three collections in the British Museum (Natural History) [BMNH]: the collection made by Hugh Scott in North and South Yemen, recently supplemented by spirit material collected by Peter Heath in the environs of Taizz, N. Yemen in 1978–9; material obtained by the author from Dhofar in 1976; and a comprehensive collection made throughout Oman by Major Michael Gallagher from 1976 onwards.

Additional material, including many important types, has been loaned from the following institutions: Muséum National d'histoire Naturelle, Paris [MNHN]; Royal Scottish Museum, Edinburgh [RSM]; Zoological Museum, Copenhagen [ZMC]; Muséum d'histoire Naturelle, Geneva [MHNG]; Academy of Natural Sciences, Philadelphia [ANS]; National Museum of Wales, Cardiff [NMW]; and Zoologisches Museum, Berlin [ZMB].

All conchological measurements are expressed in millimetres as follows: shell height × max. shell width × min. shell width;   aperture height × aperture width;   lip width (if developed); number of whorls.
e.g.   23·1 × 10·2 × 9·4;   9·5 × 7·0;   lip 1·2;   6·7 wh.

Considerable problems have been encountered with Arabic place names and several localities could not be traced. In particular it has not proved possible to determine the precise location of 'Senna', the type locality of Cerastus dinshawi Sykes, 1903; nor a number of Waterson's localities in Saudi Arabia and Yemen. In the lists of material, locality names have been copied directly from the original labels in almost all cases, but in discussing distributions in the text, spelling have usually been taken from the comprehensive edition of the Times Atlas of the World, 1968. In particular, the Yemen Arab Republic is referred to as Yemen and the Peoples Republic of South Yemen (formerly the Western Aden Protectorate) as South Yemen. Muscat and Oman is simply called Oman. Maps of south-western Arabia and of northern Oman showing the principal locations are given in Figs 1 and 2.
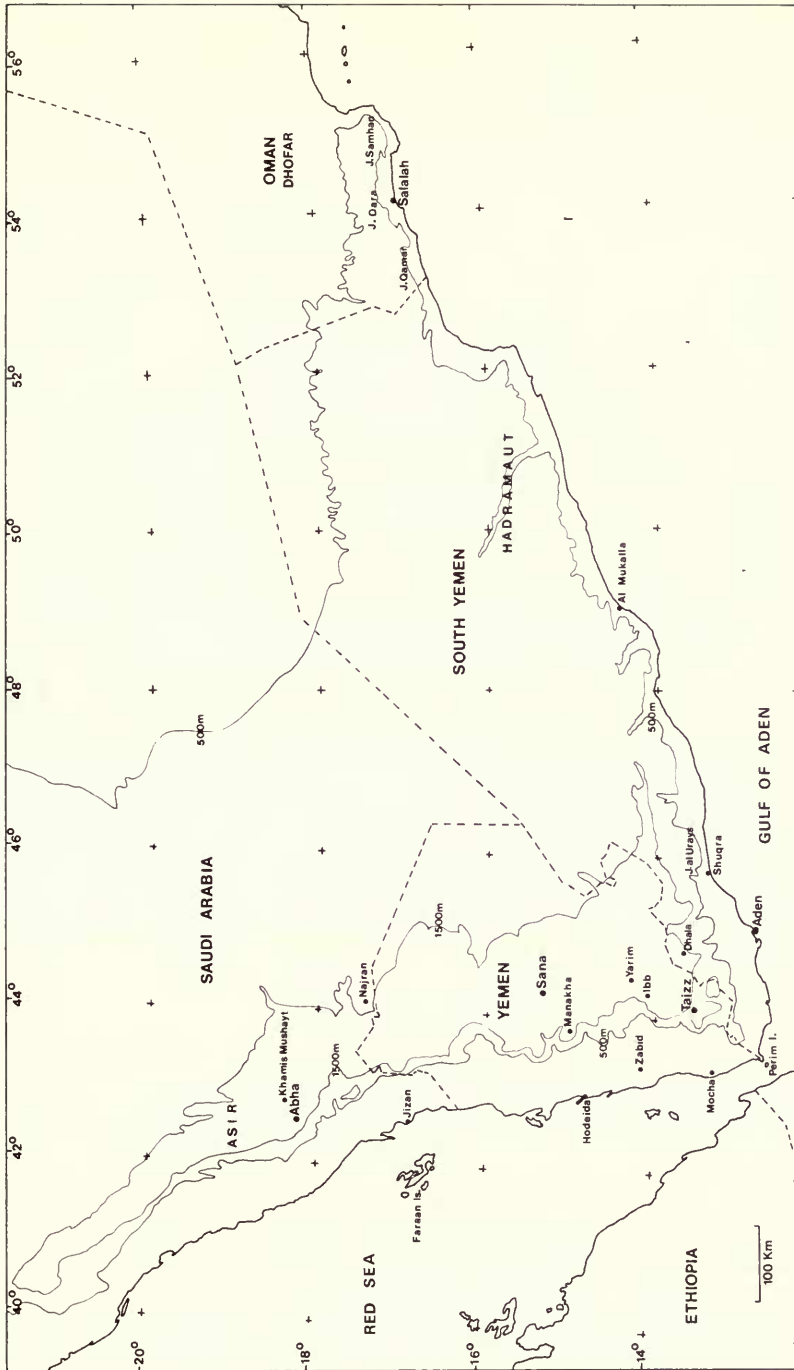
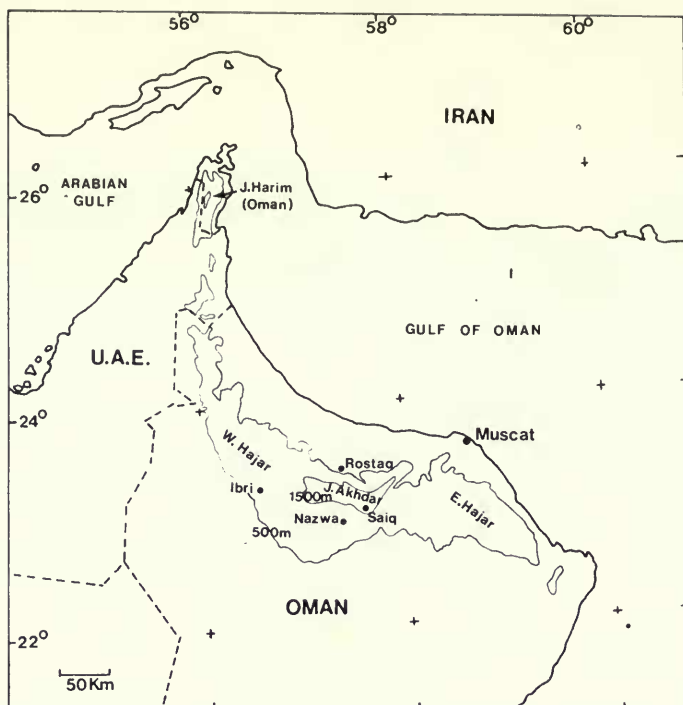**Fig. 1** Map of south-west Arabia showing principal locations.

Fig. 2   Map of northern Oman showing principal locations.

Systematic account

Family **ENIDAE** *sensu lato*

Subfamily **CHONDRULINAE** Wenz, 1923

DIAGNOSIS. Kidney orthurethrous, lung with short renal groove but lacking rectal fold. Hermaphrodite duct with clump of culs-de-sac above seminal vesicle; spermoviduct with serous canal; penis without appendix.

MASTUS Beck, 1837

TYPE SPECIES. *Helix pupa* Brugière [subs. desig. Herrmannsen, 1847].

DIAGNOSIS. Penis without appendix, but with large, pointed papilla. Spermatheca with diverticulum.

Mastus omanensis (Smith, 1894)

Buliminus omanensis Smith, 1894:141, fig. 1. [Green Mountain, Oman].
Buliminus omanensis Smith. Smythe & Gallagher, 1977:223, pl. 1.

TYPE MATERIAL. Lectotype (here designated, BMNH 1894.3.22.5) and 4 Paralectotypes (BMNH 1894.3.22.6–9), Green Mountain, (Jebel Akhdar, Oman), leg. Jayakar.

OTHER MATERIAL. **Oman:** Nazwa, leg. Jayakar, BMNH 1900.6.8.39–41, (3 specs.); Yika, 400 m., leg. M. D. Gallagher, 19.xi.1976, BMNH, (16 specs, 4 dissected); Ghafdi, Wadi Bani Ghafir, 400 m., leg. M. D. Gallagher, BMNH, (24 specs, 2 dissected); Gabet Al Habina, 2100 m., leg. M. D. Gallagher, 29.xi.1977,
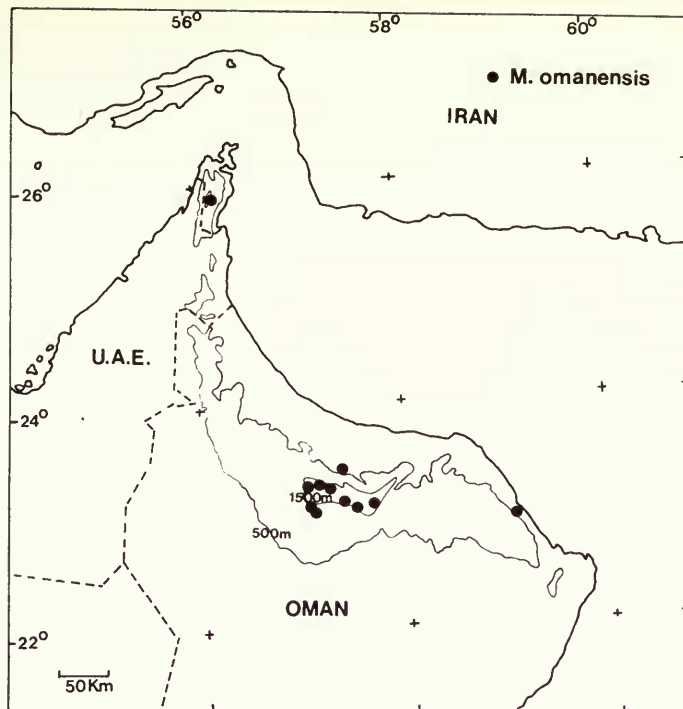
Fig. 3   Distribution map of *Mastus omanensis*.

BMNH, (23 specs.); Jabal Sirah, 2200 m., leg. M. D. Gallagher, 12.vii.1977, BMNH, (1 spec.); 15.v.1978, BMNH, (6 specs.); Jabal Harim, Ruus al Jibaal, 1800–2000 m., leg. M. D. Gallagher & J. P. Manderville, 27.ii.1979, BMNH, (8 specs, 1 spirit); Quasaydot, Ruus al Jibaal, 950 m., leg. M. D. Gallagher, 5.iii.1979, BMNH, (1 shell fragment); Jabal Akhdar, 1400 m, leg. M. D. Gallagher, 8.vi.1979, BMNH, (1 spec.); Jabal Kawr, 2800 m, leg. R. P. Whitcomb, 22.x.1979, BMNH (1 spec.); Wadi Saiq, 1800 m, leg. M. D. Gallagher, 21.iii.1981, BMNH (15 specs.); Wadi Harabin, E. Hajar Mts., 110 m, leg. M. D. Gallagher, 28.viii.1981, (3 specs.); Wakan, leg. M. D. Gallagher, 26.iii.1982, BMNH, (6 specs, 1 dissected).

DISTRIBUTION (Fig. 3). With the exception of synanthropic lowland sites (between 110–400 m above sea level) such as Yika, Ghafdi and Wadi Harabin (all cultivated habitats), the species appears to be restricted to areas above 1500 m in the Jebel Akhdar and Jebel Harim ranges of northern Oman.

DESCRIPTION. Dextral, cylindrical conic *with blunt, rounded apex*; surface glossy with irregular transverse striae and numerous fine, denser spiral striae; protoconch smooth; umbilicus closed. Aperture oval with reflexed lip; callus often extending across parietal wall. Colour uniform pale brown to opaque white, protoconch darker brown.

Shell. Dimensions of Lectotype (Fig. 4a): 23·9 × 12·2 × 9·7; 12·1 × 9·8; lip 2·2; 6·9 wh. Paralectotypes: 21·2 × 11·2 × 9·5; 10·8 × 7·7; lip 2·0; 6·5 wh.;   21·6 × 11·9 × 9·0; 10·8 × 8·1; lip 1·6; 6·6 wh.;   21·9 × 1·9 × 9·3; 10·8 × 8·9; lip 1·9; 6·6 wh.;   20·2 × 11·4 × 9·0; 11·0 × 8·5; lip 1·9; 6·1 wh.

Although there was generally rather little variation in shell size, and more particularly shape (Table 1), a sample of three shells from Wadi Harabin in the eastern Hajar mountains were quite exceptionally small, the dimensions of the smallest adult shell being: 12·3 × 7·3 × 6·9; 6·9 × 5·6; lip 1·2, wh. 5·3. This may be accounted for by the extremely low elevation of the site, 110 m, where moisture levels are almost certainly considerably lower than at the more usual elevations for this species of between 1500–3000 m, even though the locality was a terraced cultivation.
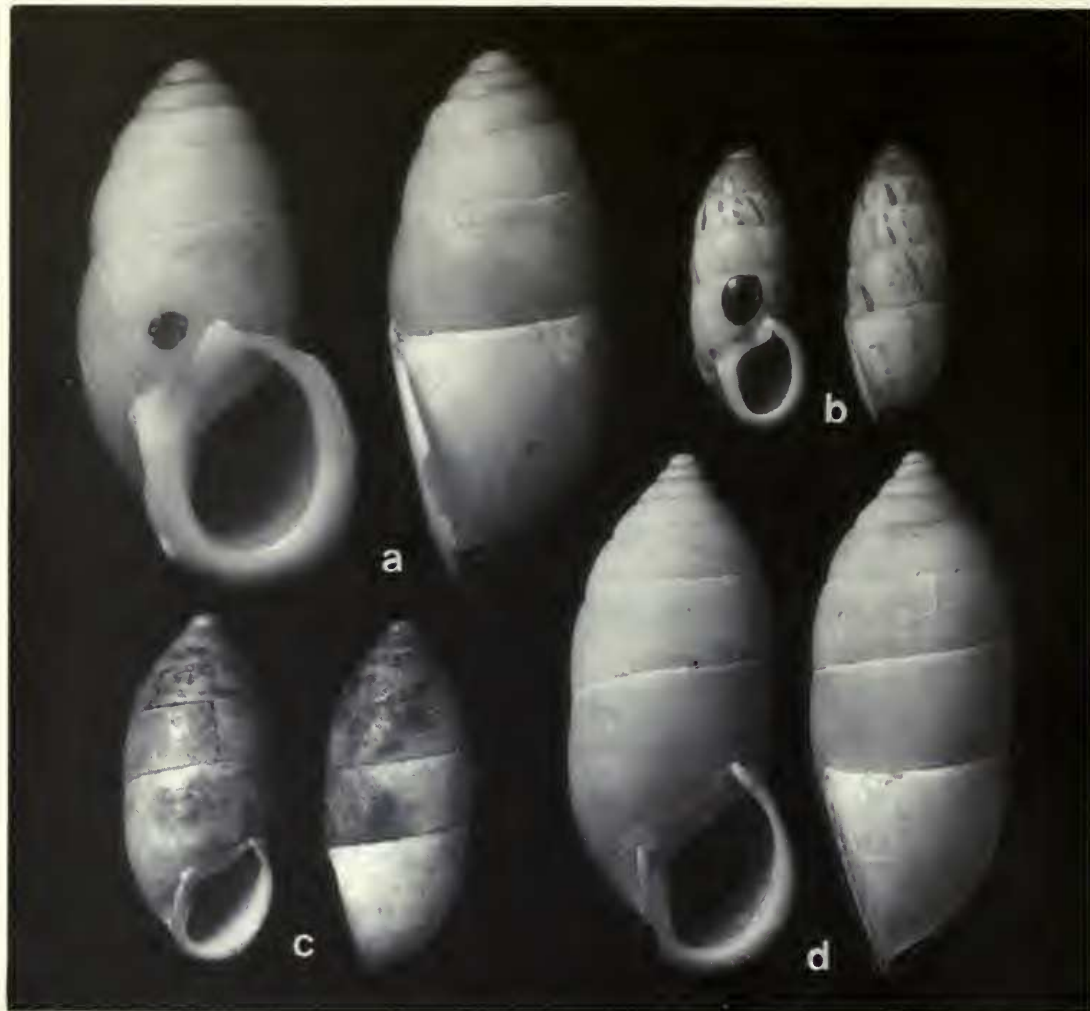
Fig. 4 a, Lectotype of *Buliminus omanensis* Smith, BMNH 1894.3.22.5; b, lectotype of *Buliminus jousseaumei*, BMNH 1894.3.22.10; c, holotype of *Buliminus hedjazicus* Bourguignat, MHNG; d, lectotype of *Bulimus sabaeanus* Bourguignat, MHNG. All × 3.

Table 1 Comparison of shell dimensions of living *Mastus omanensis* from sites in Jebel Akhdar, northern Oman, using Analysis of Variance.

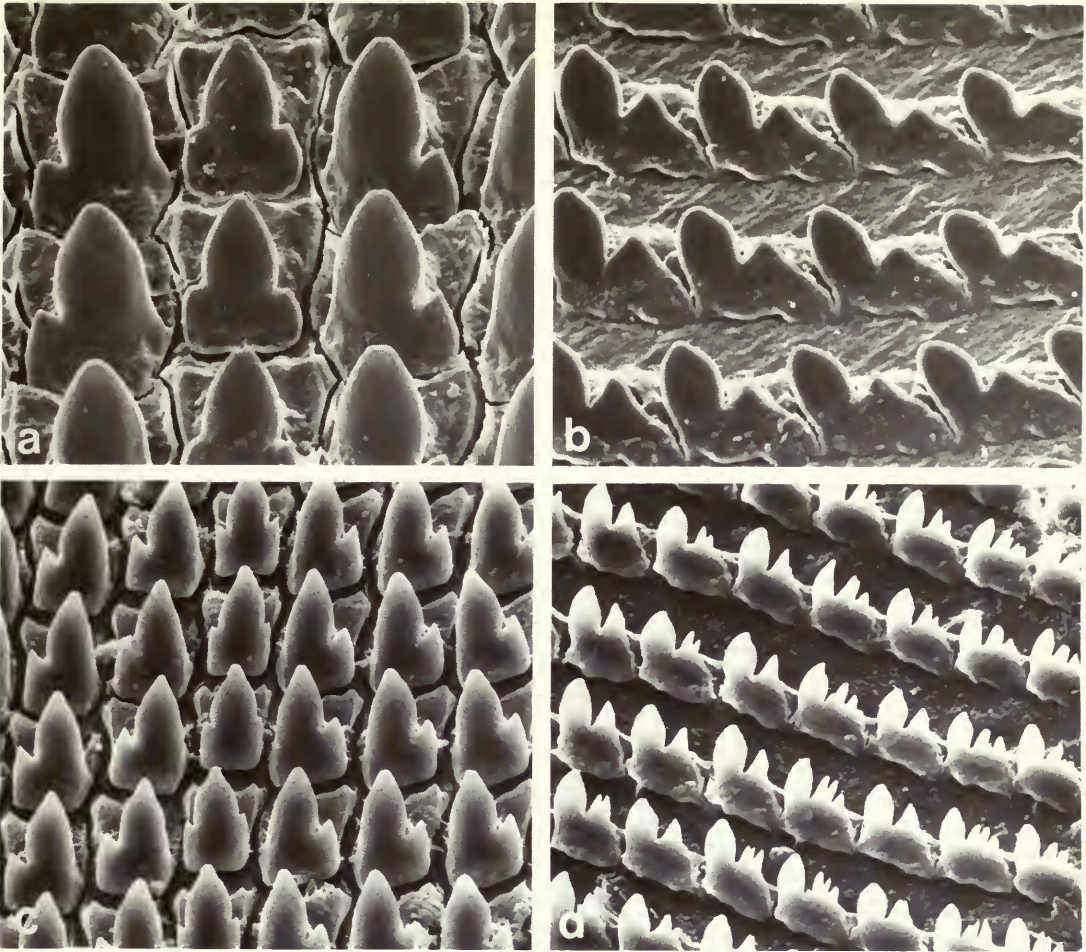| Parameter	Yika, 19.xi.1976 (n = 7)		Wakan, 26.iii.1982 (n = 6)		Ghafdi, 29.xi.1977 (n = 6)		F (d.f. 2, 16)	
	x	sd	x	sd	x	sd		
Shell ht..	17·83	1·26	19·62	0·92	18·0	0·93	4·53	*
Shell diam.	10·70	0·3	10·76	0·6	10·28	0·34	2·78	ns
Apert. ht.	9·3	0·61	9·95	0·95	9·55	0·51	1·14	ns
Apert. diam.	7·67	0·6	7·85	0·56	7·75	0·45	0·14	ns
Spire Index	1·75	0·11	1·83	0·11	1·75	0·07	1·35	ns

* = p < 0·05
ns = not significant.

Fig. 5 Radular teeth of northern Oman Enidae: a, *Mastus omanensis,* Yika, 19.xi. 1976, central and lateral; b, marginal; c, *Imparietula jousseaumei,* Rostaq, central and lateral; d, marginal; × 720.

Body. Uniformly cream in colouration.

Radula. (Figs. 5a–b; Table 2). Central tooth noticeably smaller than laterals, and ectocones of central relatively reduced. Marginal teeth with very blunt mesocone and wide, pointed ectocone which only becomes bicuspid in last three or four teeth in row. Basal plates quadrate and extremely broad.

Lung cavity (Fig. 6A). Similar in morphology to *Imparietula jousseaumei,* but occupying only a little over one whorl (Table 3); relatively longer kidney extending 0·95 times cavity length. A shallow groove runs from renal orifice along kidney almost to its apex. Mantle gland much less prominent than in *jousseaumei;* outer lung wall unpigmented.

Reproductive system (Figs 7A–B, 8C–D). Hermaphrodite gland comprising between five and seven lobes connected linearly to hermaphrodite duct, which bears clump of *culs-de-sac* and massively developed seminal vesicle (Fig. 8D). Talon short, simple and slightly curved; at its point of entry on spermoviduct is a large sac or caecum (Fig. 8C). Spermoviduct only slightly longer than free oviduct, which in turn is about twice length of vagina. Spermatheca with long, strong diverticulum which is continuous with basal stalk, and of equal thickness; spermatheca

Table 2 Tooth number and size from steroscan preparations and published data. Measurements are taken to the nearest 0·5 micron.

Species	Locality	No. per half row			Width	
		total	lat.	marg.	central	lateral
Euryptyxis candida	Taizz, 1979	40–42	13–14	26–28	26·0–26·5	28·0–28·5
	Menaha*	50	—	—	—	—
E. fragosa	Taizz, 1979	40–42	14–15	26–27	28·0–29·0	28·0–29·0
E. labiosa	Tawai Atair, 1978	31–33	13	18–20	28·0–28·5	29·0
E. latireflexa	Ain Arzat, 1976	39–41	13–15	26–27	23·0–23·5	23·0–24·0
	Tawai Atair, 1978	38–39	13	25–26	27·0–27·5	27·5–28·0
Cerastus schweinfurthi	Jabal Sumara, 1974	38	10	28	20·5	25·0
	Menaha*	43	—	—	—	—
C. scotti	Jebel Jihaf, 1937†	33	—	—	—	—
C. girwanensis	Jebel Girwan, 1938†	23	—	—	—	—
Zebrinops albatus	Taizz, 1978	26–27	10	16–17	16·5–17·0	19·0–19·5
	Taizz, 1937†	38	—	—	—	—
Z. 'ventricosa'	Dhala, 1937†	29	10	19	—	—
Imparietula jousseaumei	Rostaq, 1976	26–27	10	16–17	21·0–22·0	24·5–25·0
Mastus omanensis	Yika, 1976	24–26	11–12	13–15	11·0–12·0	13·5–14·0

*from Hesse, 1933
†from Connolly, 1941

proper continues as thin side-branch with large, globular head. Inserting at base of vagina and atrium is well-developed atrial retractor muscle.

Epiphallus inserting on penis apically with short flagellum at point of entry of vas deferens. A short retractor muscle inserts laterally on penis, and originates on lower lung wall. Within penis is a hollow papilla or verge occupying most of lumen (Fig. 7B), resembling Hesse's figure of the penial papilla of *Mastus pupa* (Hesse, 1933: fig. 2D). Penial appendix absent.

Two spermatophores were recovered and were closely similar in size and shape (Fig. 9B). Spermatophore approximately 10 mm long and 0·3–0·4 mm wide; pointed at anterior end and bearing a complex spiral fin at other. Rich corneous brown in colour. Both recovered from within spermatheca, and oriented with pointed end inserted into diverticulum.

COMMENTS. The reproductive anatomy of *omanensis* appears sufficiently similar to that of *Mastus* to be included within that genus; although differing in lacking the short median epiphallar caecum of *Mastus pupa,* it does agree in possessing a relatively large penial papilla and a short, blunt terminal epiphallar flagellum.

Of related genera, *Adzharia* Hesse is characterised by an elongate flagellum on the epiphallus (Hesse, 1930: 158), and *Chondrula* Beck and *Swertzowia* Kobelt by apertural dentition, neither of which is found in *omanensis*.

Subfamily ENINAE Pilsbry & Cooke, 1914

DIAGNOSIS. Kidney orthurethrous; lung with short renal groove, but lacking rectal fold. Hermaphrodite duct with clump of culs-de-sac above seminal vesicle; spermoviduct with serous canal; penis with diverticulum.
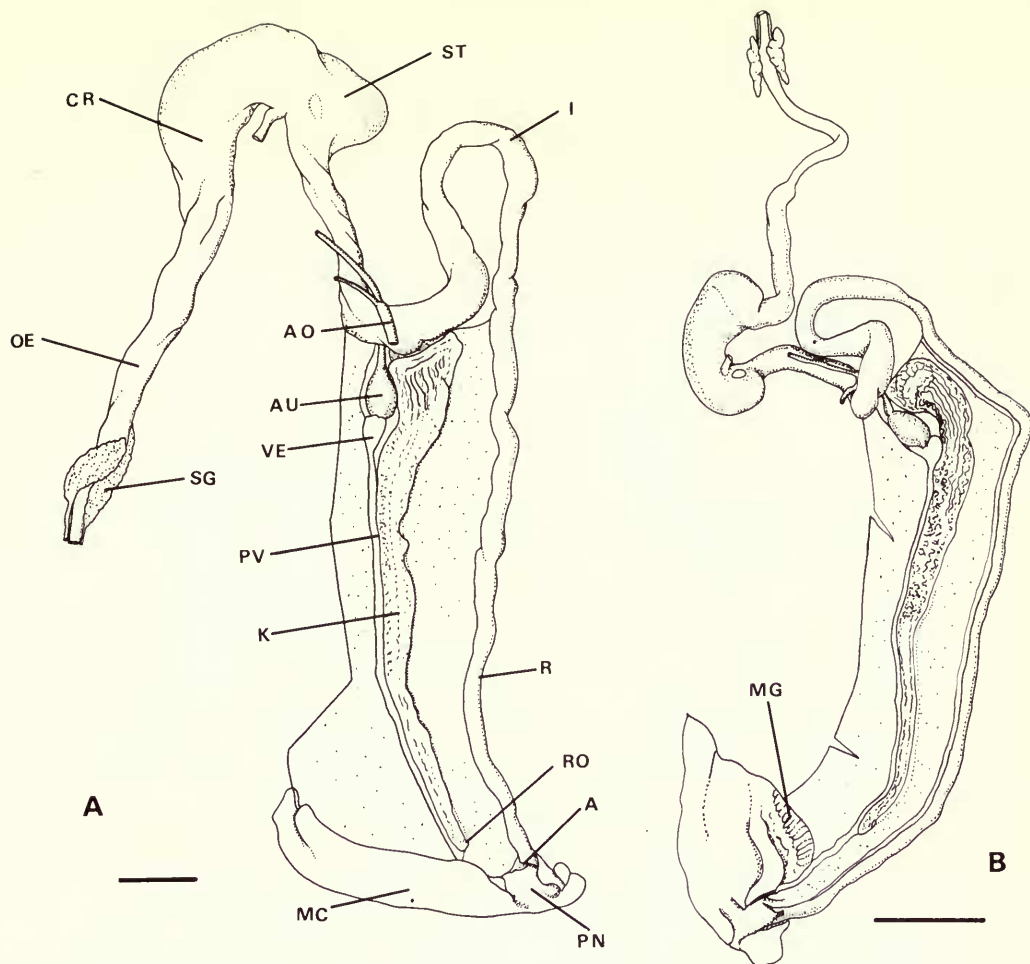
Fig. 6 Lung and alimentary system of A, *Mastus omanensis,* Yika, Oman, 1976; B, *Imparietula jousseaumei,* Saiq, Oman, 1980. Scale 2 mm.

Table 3 Length in whorls of the various regions of the visceral mass.

| Species	Locality	Lung	Lung/ stomach	Stomach/ dig. gland	Total visc. mass	Shell
M. omanensis	Yika, 1976	1·1	1·1	2·4	4·6	5·9
	Ghafdi, 1976	1·2	1·1	2·5	4·8	6·0
I. jousseaumei	Ibri, 1977	1·8	1·2	3·4	6·5	7·0
	Saiq, 1981	1·9	1·1	2·5	5·5	6·2
E. candida	Taizz, 1979	1·2	0·7	2·6	4·5	6·8
E. fragosa	Taizz, 1979	0·8	1·1	2·4	4·3	7·0
	Taizz, 1946	1·1	0·9	2·7	4·7	7·4
E. labiosa	Tawi Atair, 1978	1·2	0·8	1·7	3·7	6·5
E. latireflexa	Ain Arzat, 1976	1·0	0·9	2·1	4·0	7·1
	Dahaq Thuari, 1977	1·3	1·0	1·6	3·9	6·7
Z. albata	Taizz, 1978	1·1	1·0	4·0	6·1	7·3
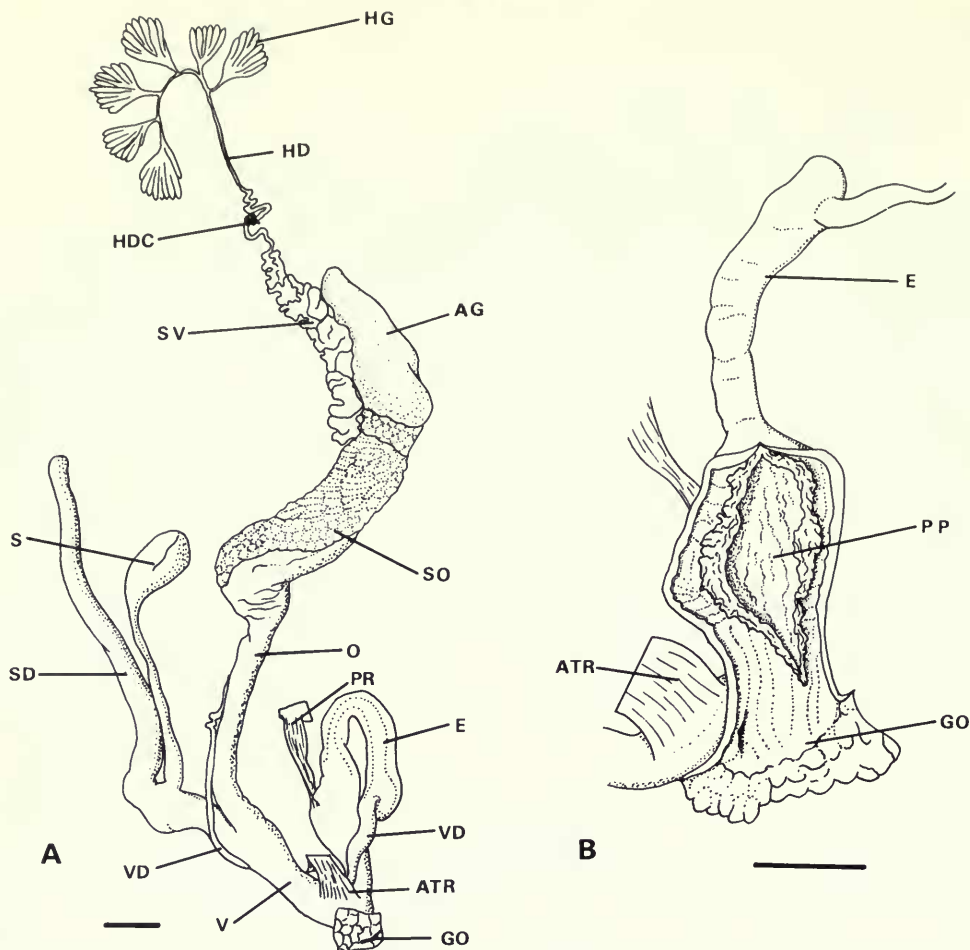
Fig. 7 *Mastus omanensis*, Yika, Oman, 1976: A, genital system; B, penis and epiphallus. Scale 1 mm.

IMPARIEṬULA Lindholm, 1925

(= *Pseudochondrula* Hesse, 1933)

TYPE SPECIES. *Bulimus leucodon* Pfeiffer [orig. desig.].

DIAGNOSIS. Penis with appendix and short, blunt papilla; epiphallus with short median caecum. Spermatheca without diverticulum.

Imparietula jousseaumei (Smith, 1894)

Buliminus jousseaumei Smith, 1894:142, fig. 2. [Oman].
Buliminus (Subzebrinus) dautzenbergi Ancey, 1906:262. *Nom. nov. pro B. jousseaumei* Smith.
Buliminus jousseaumei Smith. Smythe & Gallagher, 1977:223.
Ena schahrudensis (Boettger). Smythe & Gallagher, 1977:223.

TYPE MATERIAL. Lectotype (here selected, BMNH 1984.3.22.10) and Paralectotype (BMNH 1894.3.22.11); 5 possible Paralectotypes, mixed with the former (BMNH 1900.8.8.69–73), 'Oman', leg. Jayakar.
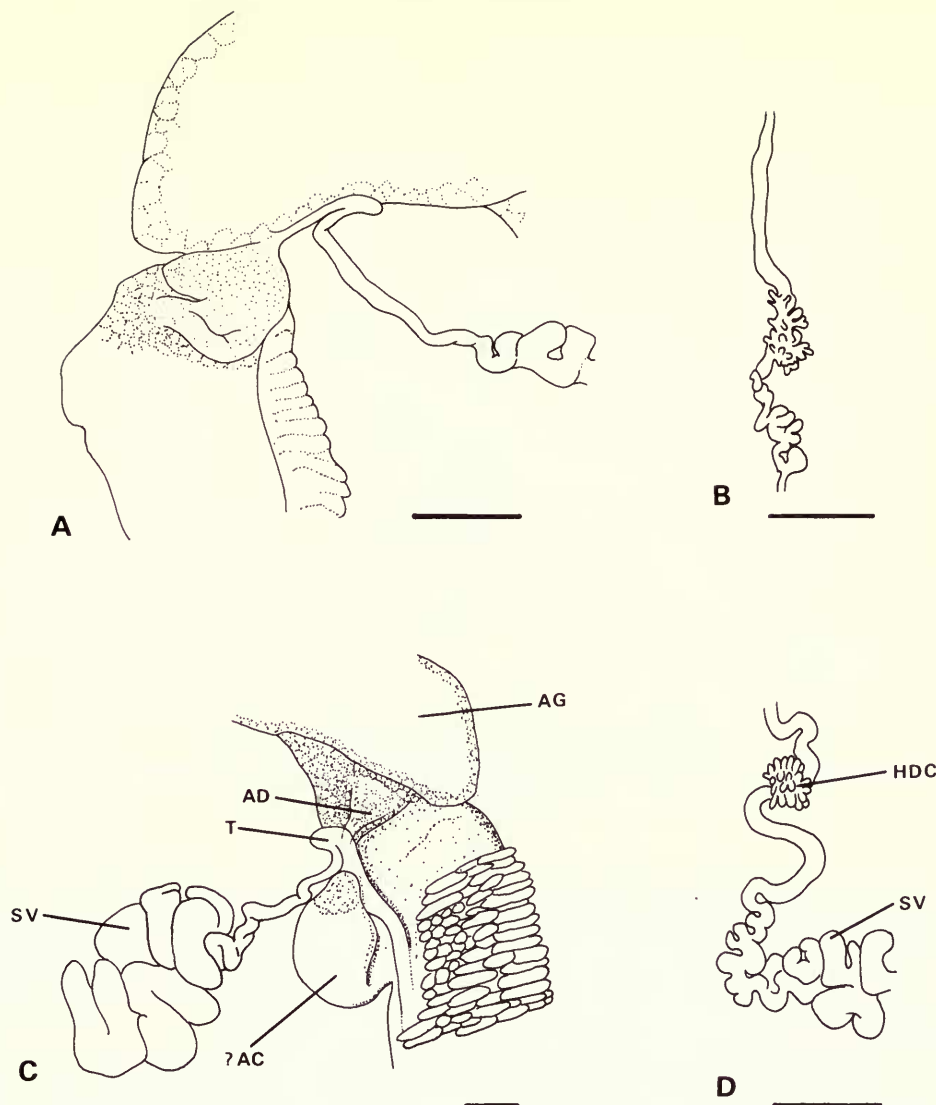
Fig. 8 *Imparietula jousseaumei,* Saiq, Oman, 1980: A, talon region; B, hermaphrodite duct. *Mastus omanensis,* Yika, Oman, 1976. C, talon region; D, hermaphrodite duct. Scale 0·5 mm.

OTHER MATERIAL. **Oman:** Mazra Qid, 488 m., leg. M. D. Gallagher, 15.xi.1976, BMNH, (9 specs., 2 dissected); Rostaq, 350 m., leg. M. D. Gallagher, 17.xi.1976, BMNH, (13 specs, 1 dissected); leg. R. P. Whitcombe, 12.ii.1979, (3 specs., spirit); Yika, c. 400 m., leg. M. D. Gallagher, 19.xi.1976, BMNH, (numerous specs., 2 dissected); Shafdi, Wadi Bani Ghafir, leg. M. D. Gallagher, 20.ix.1976, BMNH, (1 spec., spirit); Ibri, leg. M. D. Gallagher, 24.xi.1977, BMNH, (numerous specs., 1 dissected); Jabal Sira, 2200 m., leg, M. D. Gallagher, 12.vii.1977, BMNH, (8 specs.); 15.iv.1978, BMNH, (numerous specs., 4 spirit, 1 dissected); Sulaif, leg. M. D. Gallagher, 24.xi.1977, (6 specs.); Wadi Hilm, 100 m., leg. M. D. Gallagher, 15.iv.1978, BMNH, (3 specs.); Wadi Harabin, Eastern Hajar Mts., 125 m., leg. M. D. Gallagher & D. P. Mallon, 26.x.1979, BMNH, (numerous specs.); Jabal Kawr, 2800 m., leg. R. P. Whitcomb, 22.x.1979, BMNH, (3 specs.); Mudaybi, 300 m., leg. M. D. Gallagher & D. P. Mallon, 5.xi.1979, (1 spec.); Jabal Sham, 2980 m., leg. M. D. Gallagher, 20.i.1980, BMNH, (11 specs.); Wakan, 1400 m., leg. D. P. Mallon, 15.ii.1980, BMNH, (4 specs.); Saiq Camp, 1980 m., leg. T. Larsen & M. D. Gallagher, 22.v.1980,
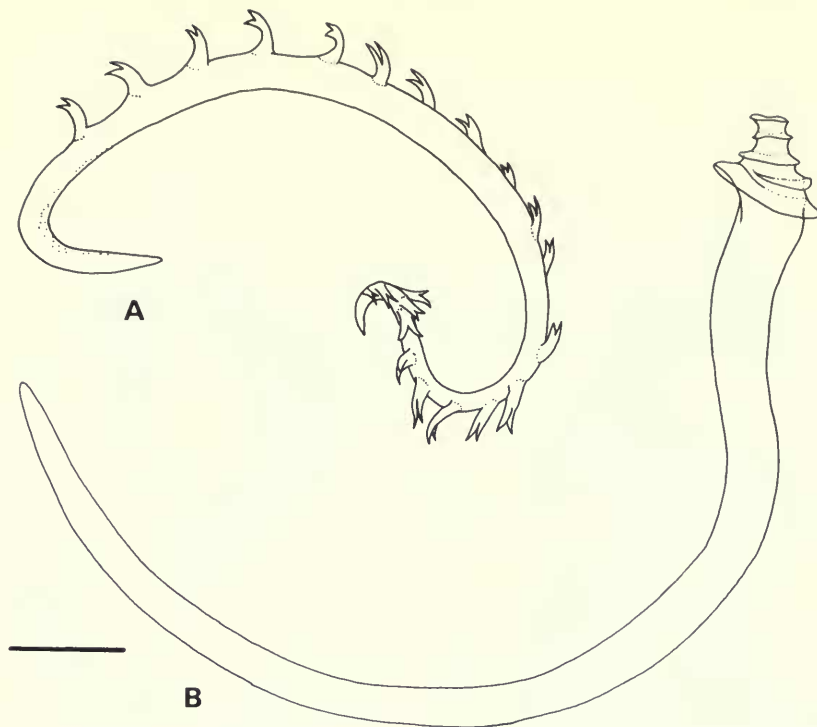
Fig. 9   Spermatophores: A, *Zebrinops albata,* Taizz, Yemen, 1978; B, *Mastus omanensis,* Yika, Oman, 1976. Scale 1 mm.

BMNH, (numerous specs., 3 dissected); leg. M. D. Gallagher, 21.v.1981, 1800–1860 m., BMNH, (numerous specs.); Jabal Aswad, Sharqiya, 1850 m., leg. M. D. Gallagher, 8.iii.1980, BMNH, (5 specs.); Tanuf, 600 m., leg. M. D. Gallagher, 20.iii.1981, BMNH, (5 specs.); Wadi Far, near Rostaq, leg. R. M. Lawton, ii.1982, BMNH, (1 spec.); Wadi Duwaykhilah, 1800 m., leg. M. D. Gallagher, 12.iii.1982, BMNH, (9 specs.); Wakan, 1500 m., leg. M. D. Gallagher, 26.iii.1982, BMNH, (numerous specs.).

DISTRIBUTION (Fig. 10). Widely distributed in the northern Oman mountains from the summit of Jabal Akhdar (2980 m) to the foothills; also recorded at a number of lowland synanthropic habitats down to 100 m in the eastern Hajar Mountains. It has not been recorded from Jebel Harim.

DESCRIPTION. Dextral, elongate pupiform, with tapering blunt apex; surface glossy with fine irregular transverse striae and occasional faint spiral striae; protoconch smooth and glossy. *Distinct columellar fold in the body whorl.* Whorls slightly rounded sutures shallowly impressed; umbilicus closed. Aperature oval; lip reflected and flattened, sometimes slightly reflexed at margin, *continuous across parietal wall and internally notched at the parietal/palatal junction. Colour transparent pale brown with irregular transverse opaque white streaks becoming progressively thicker towards the aperature*; protoconch brown; lip white.

Shell. Dimensions of Lectotype (Fig. 4b): 12·1 × 5·3 × 4·5; 4·8 × 3·9; lip 0·8; 7 wh. Remaining type series: 10·7 × 5·5 × 4·9; 4·7 × 4·0; lip 0·8; 6·2 wh.; 12·4 × 5·3 × 4·6; 4·9 × 3·9; lip 1·0; 7 wh.;   11·2 × 5·3 × 4·6; 5·0 × 3·9; lip 0·8; 6·4 wh.;   11·4 × 5·0 × 4·4; 4·5 × 3·7; lip 0·8; 6·4 wh.;   11·9 × 5·4 × 4·8; 4·8 × 3·6; lip 0·8; 6·7 wh.;   10·9 × 5·4 × 4·8; 4·8 × 4·1; lip 0·8; 6·3 wh.

This species appears to show rather greater geographical variation in shell morphology than *Mastus omanensis,* whilst maintaining considerable within-population homogeneity. Six living
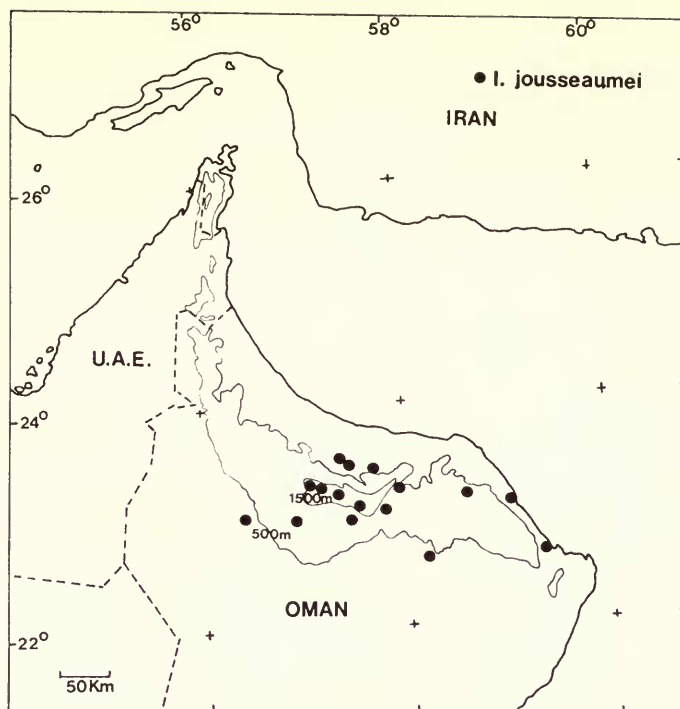
Fig. 10   Distribution map of *Imparietula jousseaumei*.

populations were examined, using analysis of variance (Table 4), the results proving significant for all shell parameters.

Body. Surface pale, almost colourless, but top of tubercules may be 'peppered' with grey or brown pigmentation.

Radula (Figs 5c–d). Teeth relatively slender in comparison with *Mastus omanensis* but only slightly fewer in number (Table 2). Unlike *omanensis*, marginal ectocones of *jousseaumei* commonly develop multiple cusps.

Lung cavity (Fig. 6B). Of the typical enid type with only a weak groove leading from renal pore to about half-way back along kidney margin. Kidney extends about 0·8 times length of entire lung. Venation very weak and bearly visible, but well-developed mantle gland present. Total lung cavity occupies 1·8–1·9 whorls (Table 3).

Reproductive system (Figs 8A–B, 11). Hermaphrodite gland composed of three or four lobes imbedded in digestive gland; duct bears clump of *culs-de-sac* above seminal vesicle (Fig. 8B), and terminates as talon formed from simple convolution of duct without any appendages. At point of entry of talon is a large sacculate structure (Fig. 8A) as in *Mastus omanensis*, similar to the albumen chamber of *Orcula* (Steenberg, 1925: pl. VIII). Albumen gland relatively short, about 2/3 length of spermoviduct, and about half length of the simple spermatheca. Epiphallus greatly modified, bearing blunt caecum about half-way along its length and a short terminal flagellum. Spermatophore unknown but epiphallus internally complex (Fig. 11B). Epiphallus enters penis apically through rounded papilla.

Penis has six, symmetrically arranged longitudinal pilasters, each with enlarged portion at top, separated from main body of pilaster by slight constriction; penis waisted at this point. Tops of pilasters form six-pointed coronet on tip of everted penis (Fig. 11C). Retractor muscle inserts laterally about half-way down penis on opposite side to appendix; latter of typical pupillacean

Table 4   Comparison of shell dimensions of living *Imparietula jousseaumei* from sites in northern Oman using Analysis of Variance.

Parameter	Yika, 19.xi.76 (n=10) 400 m.		J. Sira, 15.vi.78 (n=7) 2750 m.		Ibri, 24.xi.77 (n=10) 600 m.		Saiq, 22.v.81 (n=7) 1980 m.		Rostaq, 17.xi.76 (n=6) 350 m.		Wakan, 22.iii.82 (n=7) 1500 m.		F
	x	s.d.	x	s.d.	x	s.d.	x	s.d.	x	s.d.	x	s.d.	(d.f. = 5,41)
Shell ht.	11·35	0·31	11·9	0·44	11·58	0·6	10·97	0·46	11·21	0·58	12·58	1·15	3·67**
Shell diam.	5·02	0·12	4·54	0·25	5·2	0·38	4·6	0·29	4·46	0·36	5·46	0·36	9·17***
Apert. ht.	4·36	0·19	4·14	0·18	4·58	0·25	4·15	0·09	4·41	0·25	4·45	0·34	4·02**
Apert. diam.	3·48	0·26	3·3	0·25	3·64	0·18	3·27	0·1	3·63	0·19	3·5	0·29	3·28*
Spire Index	2·27	0·22	2·61	0·11	2·31	0·2	2·4	0·24	2·1	0·15	2·3	0·09	5·41***

***p<0·001
**p<0·01
*p<0·05
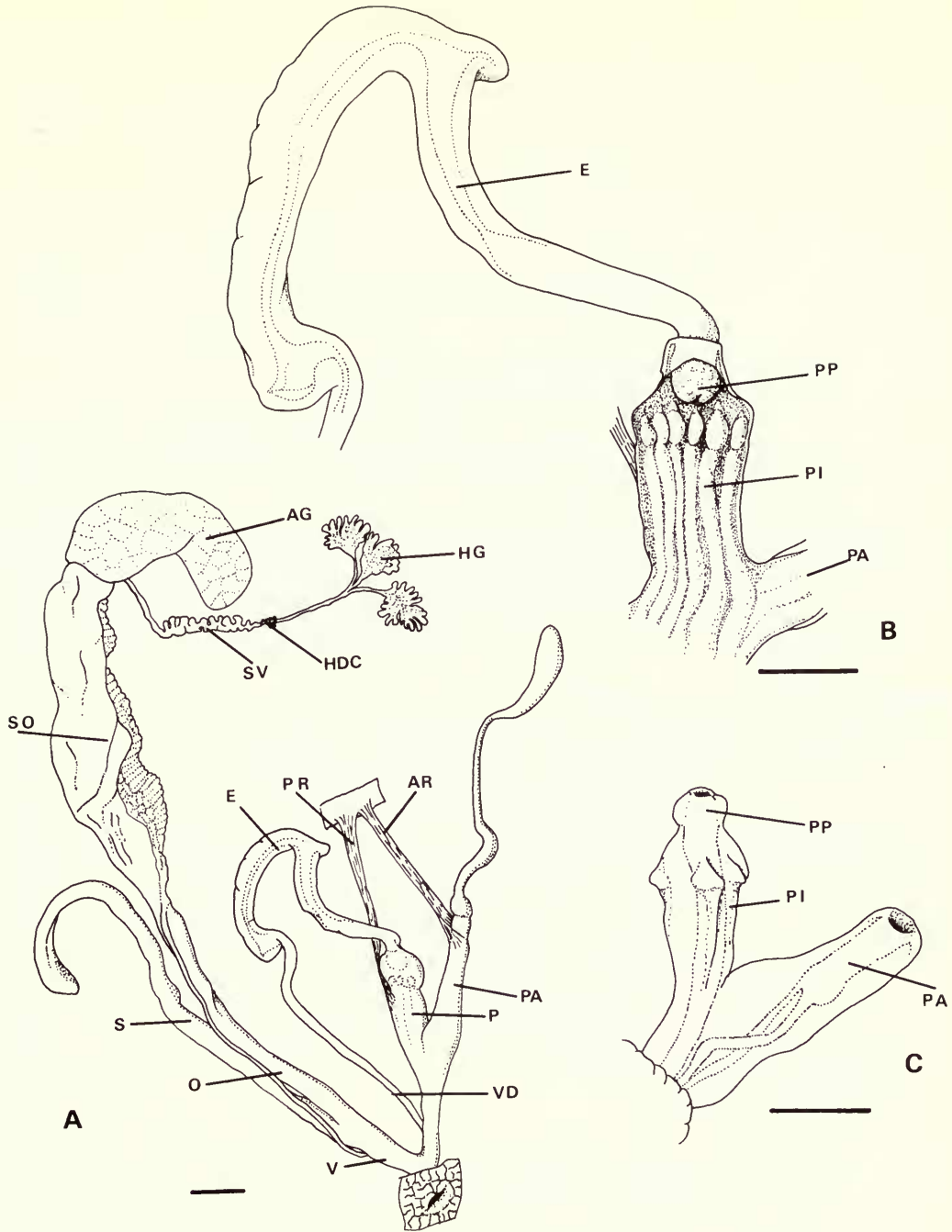
Fig. 11 *Imparietula jousseaumei,* Saiq, Oman, 1980: A, genital system; B, penis and epiphallus; C, everted genitalia. Scale 1 mm.

structure but relatively short (about 3–4 times length of penis). Appendicular retractor muscle inserts slightly below top of basal portion and originates next to but separate from penis retractor, on lower lung wall; base of appendix without strong pilasters. Atrium short and undifferentiated internally.

COMMENTS. The absence of a spermathecal diverticulum, combined with the presence of a penial appendix and an epiphallus with a short terminal flagellum and blunt median caecum, which inserts apically on the penis, place this species within *Imparietula*. Conchologically it is quite distinct from any other named species of the genus (Forcart, 1940; Gittenberger, 1967). Smythe & Gallagher's (1977: 223) record of *Ena schahrudensis* from Jabal Sham is erroneous, being merely an elongate form of *Imparietula jousseaumei*.

PARAMASTUS P. Hesse, 1933

TYPE SPECIES. *Bulimus episomus* Bourguignat [monotypy].

Paramastus episomus (Bourguignat, 1857)

Buliminus episomus Bourguignat, 1857: 10, pl. 3, figs 5–7. [Nazareth].
Buliminus hedjazicus Bourguignat, 1882: 24, pl. 1, fig. 12. [between Jeddah and Mecca].
Paramastus episoma hedjazicus Bourguignat. Zilch, 1951: 42, pl. 3a, fig. 16.
?*Paramastus episomus* Bourguignat. Mordan, 1980:360, fig. 2I.

TYPE MATERIAL. Holotype, Between Jeddah and Mecca, Saudi Arabia, MHNG.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. Dextral, pupiform; surface with weak, irregular radial striae and weaker, but more regular, spiral striae, and occasional malleations, especially on body whorl; umbilicus closed. Aperture elongate oval, with flared, sharp lip; small parietal denticle near palatal/parietal boarder, and weak, broad columellar fold. Shell opaque white, but periostracum lacking.
   Shell. Dimensions of holotype (Fig. 4c): 15·2 × 6·5 × 6·4; 5·8 × 4·3; 6·7 wh.
   Anatomy. Unknown.

COMMENTS. See below under *P. sabaeanus*.

Paramastus sabaeanus (Bourguignat, 1876)

Bulimus sabaeanus Bourguignat, 1876:19 [Sabéens, near Mareb.]; Bourguignat, 1882:23, fig. 14.
Buliminus (Petraeus) sabaeanus Bourguignat. Rossmässler, 1888:31, pl. 99, fig. 560. *non sabaeanus* (Bgt.)
   Rolle & Kobelt, *in* Rossmässler, 1895–97:58, pl. 11, figs 8–11.

TYPE MATERIAL. Lectotype (here selected) and Paralectotype, Sabéens, near Mareb, Yemen, MHNG.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. As for *hedjazicus*, but aperture relatively larger and rounder, with flattened lip; spiral striae and parietal denticle absent.
   Shell. Dimensions of lectotype (Fig. 4d): 23·1 × 10·2 × 9·4; 9·5 × 7·0; 7·7 wh. Paralectotype: 21·7 × 10·0 × 8·8; 9·0 × 7·2; 7·5 wh.
   Anatomy. Unknown.

COMMENTS. The positions of this and the previous taxon at both the specific and generic levels is uncertain. Until recently both would have been referred to *Paramastus* Hesse on conchological and geographic grounds. This is still the most likely eventuality and they are provisionally retained here. However, Heller (1971) has demonstrated that *Paramastus sensu lato* comprises two groups: one, which he named *Cyrenaicus*, lacking a penial appendix and with a distribution centered on Cyrenaica; and *Paramastus sensu stricto* possessing a penial appendix and containing with certainty only two species (*P. episomus* (Bourguignat, 1857) and *P. cyprius* Zilch, 1959). The true affinity of the Arabian snails is thus in doubt. Zilch (1951) relegated *hedjazicus* to a subspecies of *episomus* and this is retained here. Certainly both Arabian taxa fall broadly within the wide morphological range of *episomus*. Without anatomical information further speculation is valueless.

Subfamily *CERASTINAE* Wenz, 1923

DIAGNOSIS. Kidney orthurethrous; lung with well-developed renal and rectal folds. Hermaphrodite duct without culs-de-sac, and spermoviduct without serous canal. Penis with appendix.

CERASTUS Albers, 1860

TYPE SPECIES. *Bulimus distans* Pfeiffer [orig. desig.]

DIAGNOSIS. Shell lip undifferentiated or weakly flared. Penis with long, pointed caecum; penis retractor inserts on epiphallus. Penial appendix with moderately developed papilla; appendicular retractor inserts on enclosed basal portion of central stalk. Penial and appendicular retractors united prior to attachment to lung wall.

Cerastus schweinfurthi (Martens, 1895)

Buliminus schweinfurthi Martens, 1895:129. [Menaha].
Buliminus schweinfurthi var. *gracilior* Martens, 1895:129. [Menaha].
Buliminus (Cerastus) schweinfurthi Martens. Kobelt, 1902:893, pl. 127, figs 19–21; Rossmässler, 1903:51, pl. 291, fig. 1862.
Buliminus (Cerastus) schweinfurthi var. *menahensis* Kobelt, 1902:894, pl. 127, figs 22, 23. [Menaha].
Buliminus (Cerastus) schweinfurthi var. *menahensis* Kobelt. Rossmässler, 1903:52, pl. 291, fig. 1863.
Cerastus schweinfurthi Kobelt. Connolly, 1941:26.
Cerastus schweinfurthi var. *maxima* Connolly, 1941:26. [pass between Saiyani and Ibb].
Cerastua (Euryptyxis) schweinfurthi Martens. Hesse, 1933:220.
Cerastua schweinfurthii Kobelt. Verdcourt, 1974:5.
Cerastua schweinfurthii var. *maxima* Connolly. Verdcourt, 1974:5.

TYPE MATERIAL. Lectotype (here selected, BMNH 1895.8.20.1), Paralectotype (BMNH 1895.8.20.2), and 5 possible Paralectotypes (BMNH 1937.12.30.2127–31) of *schweinfirthi* Martens, Menaha, Yemen, leg. Schweinfurth. Holotype and 6 Paratypes (BMNH 1939.4.19.34–40) of var. *maxima* Connolly, Naqil Mahrras Pass, between Seyani to Ibb, Yemen, leg. Scott, 30.xii.1937, c. 2200 m.

OTHER MATERIAL. **Yemen:** Taizz District, 1250–1550 m. leg. H. Scott, BMNH 1939.4.19.53–54 (2 specs.); Wadi Dhulla, 10 km. NW. Saana, 2500 m., Leg. H. Scott, BNMH 1939.4.19.41–42 (2 specs); Thawilah, leg. L. Merucci, vi.1945, BMNH 1956.11.26–30 (5 specs + 20 unregistered); 8 km from Taizz, leg. M. Brunt & J. Mather, (1 spec); Wadi Shabau, leg. Brunt & Mather, (2 specs.); As Saiyani, 32 km N Taizz, leg. Lavranos, 1977, MNHN (9 specs); 32 km. N. Sanaa, leg. M Al-Safadi, (1 spec); Jebel Sumara, north of Ibb, 2950 m., leg. M. Lavranos, 1974, MNHN, (5 specs., 1 reconstituted and dissected).   **South Yemen:** Jebel Harir, x-xi.1937, 2300 m., 1 paratype *maxima* Connolly, BMNH 1939.4.19.27, leg. H. Scott.

DISTRIBUTION (Fig. 12). The species extends from near Dhala in South Yemen westwards to the region of Taizz, and northwards to the type locality of Menaha and to Sana. It is thus the most widely distributed Arabian *Cerastus,* and by far the most abundant in museum collections.

DESCRIPTION. Dextral; acuminate ovate, apex blunt, sutures shallow. Protoconch smooth, later with regular radial ribs; radial sculpture becoming progressively weaker, and in combination with spiral striae giving glossy appearance. Aperture not flared, slightly thickened internally, callus extending across parietal wall. Periostracum corneous olive-brown, variegated in occasional radial streaks of darker brown.

Shell. Dimensions of Lectotype, *schweinfurthi* von Martens (Fig. 13a): 31·4 × 17·4 × 1·1; 17·0 × 11·9; 7·1wh.   Dimensions of holotype, var *maxima* Connolly (Fig. 13b): 47·3 × 26·5 × 23·4; 26·2 × 18·5; 7·8 wh. Largest specimen, Wadi Shabau, Yemen, leg. Brunt & Mather: 42·7 × 25·2 × 20·6; 24·4 × 17·3; 7·3 wh.

Cerastus schweinfurthi shows considerable variation in both shell size and shape, particularly in the region between Taizz and Ibb in Yemen, from where Connolly described var *maxima*. There was a general correlation between shell size and thickness, the very largest shells being up to 1·8 mm thick.
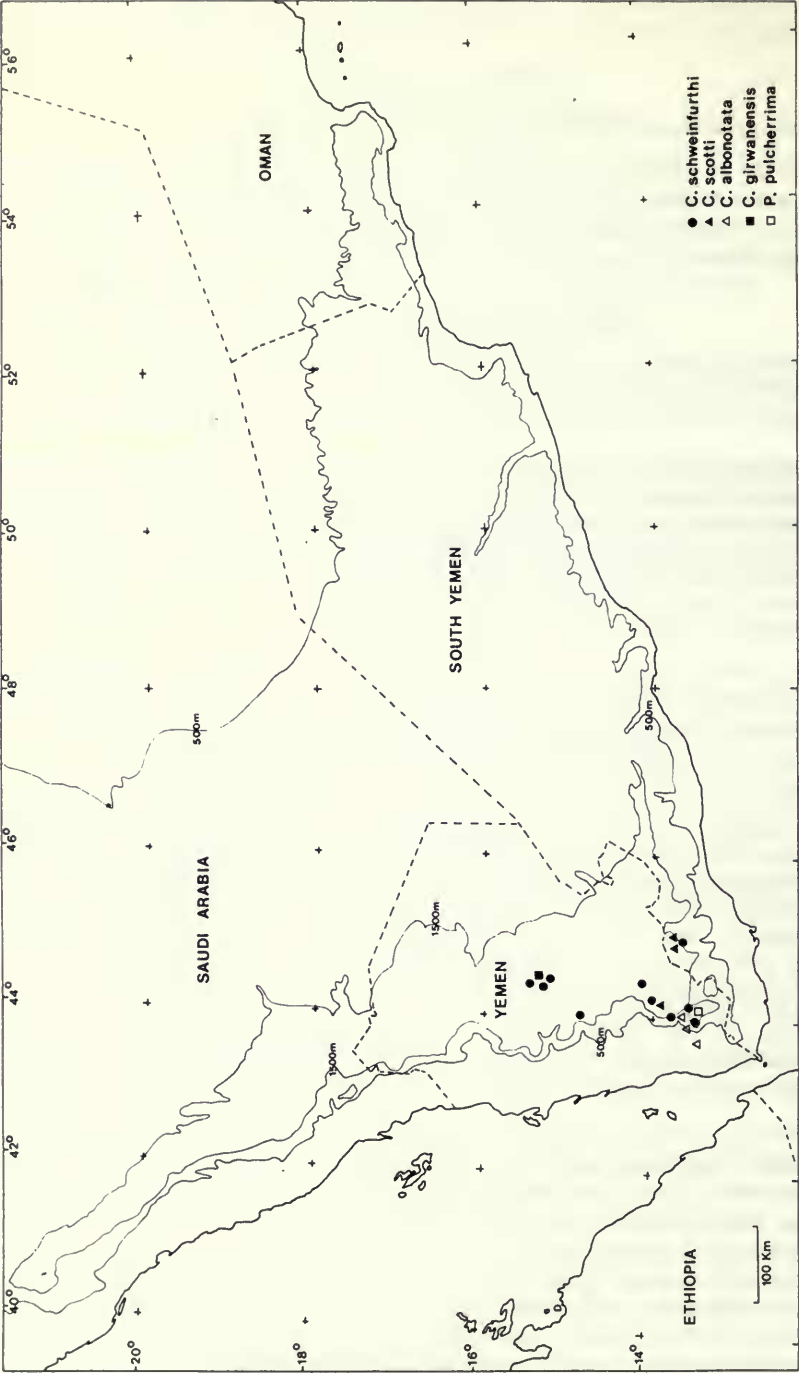
Fig. 12   Distribution map of *Cerastus* and *Polychordia.*

Fig. 13 a, Lectotype of *Buliminus schweinfurthi* Martens, BMNH 1895.8.20.1, ×1·5; b, holotype of *Cerastus schweinfurthi* var. *maxima* Connolly, BMNH 1939.4.19.34, ×1·5; c, paratype of *C. schweinfurthi* var. *maxima*, BMNH 1939.4.19.27, ×1·5; d, lectotype of *C. girwanensis* Connolly, BMNH 1934.4.19.9, ×3; e, holotype of *Cerastua albonotata* Verdcourt, BMNH 19731, ×1·5; f, holotype of *Polychordia pulcherrima* Connolly, BMNH 1939.4.19.55, ×3; g, holotype of *Cerastus scotti* Connolly, BMNH 1939.4.19.11, ×3.

Fig. 14   Radula of *Cerastus schweinfurthi*, reconstituted specimen, Jebel Sumara, Yemen, 1974: a, central and lateral teeth; b, marginal teeth; × 720.

Body. Darkly pigmented in uniform browny-black.

Radula (Fig. 14; Table 2). Part of a radula was extracted from the reconstituted specimen. Although the teeth were immature, it was possible to confirm that in all teeth the mesocones are relatively elongate, and the bases narrow in comparison with *Euryptyxis*. The marginal ectocones have a single cusp, which appears to be lacking from the outermost teeth.

Lung cavity. As far as could be established, complete renal and rectal folds are developed, united at the top of the lung. The kidney is 0·85 times the cavity length, and venation is noticeably more prominent near the mantle collar. The outer lung wall is dark brown/black with irregular patches and streaks of opaque white.

Reproductive system (Fig. 15). Hesse (1933:220–221, fig. 43.) has figured the reproductive system of *Cerastus schweinfurthi* and also gave a comprehensive description of its gross morphology. Three important features of this description are: the spermatheca which is clearly separated into head and stalk regions, the well-developed, elongate penial caecum; and the penis retractor muscle which is united with the appendicular retractor for some distance after its origin on the lower lung wall, and which inserts singly on the epiphallus. Hesse also figures a spermatophore, and a detail of a single spermatophore 'scale' (Hesse, 1933: fig. 43, D–E).

Only a single, reconstituted specimen was available for dissection in the present study. From this, it has been able to confirm many features of Hesse's description, and also describe in more detail the internal morphology of the penial appendix. It is clear (Fig. 15A) that the morphology of the junction of the basal and middle portions of the appendix is similar to *Zebrinops* although the projection of the papilla into the basal lumen is shorter. Additionally, the penial muscle sheath is single-layered. Internally, the epiphallus appeared to have spiral ornamentation and Hesse states that there is a single row of 'scales' on the spermatophore, which appears to be spirally arranged in his figure.

COMMENTS. The shell of *schweinfurthi* most closely resembles that of *Cerastus scotti* but is readily separable by its much greater size; the two species co-occur at Jebel Harir, near Dhala, South Yemen.

Cerastus albonotatus (Verdcourt, 1974)

Cerastua albonotata Verdcourt, 1974:5, figs 2a–c.

TYPE MATERIAL. Holotype, BMNH 19731, 5 miles out of Taizz, Yemen, ix.1971, leg. M. Brunt & J. D. Mather.
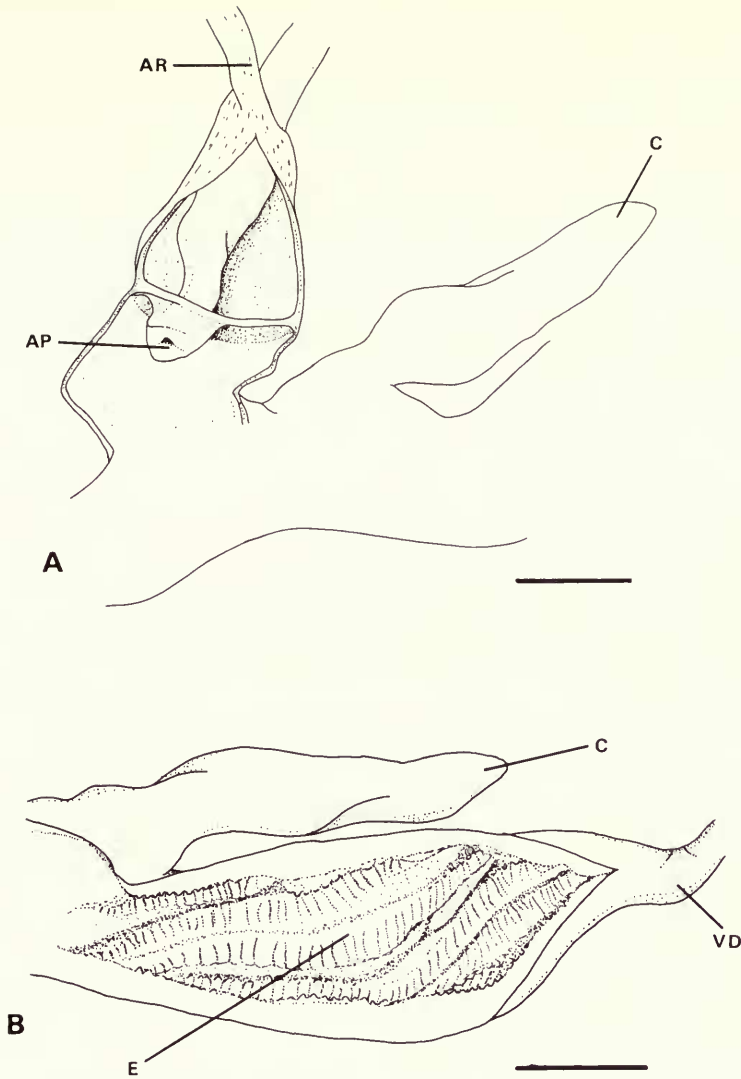
Fig. 15 *Cerastus schweinfurthi*, J. Sumara, Yemen, 1974 (Reconstituted specimen). A. Base of penial appendix; B. Epiphallus. Scale 1 mm.

OTHER MATERIAL. **Yemen:** Wadi 20 miles east of Taizz, leg. Waterson, (1 spec.) Near Taizz, 1978, leg. P. Heath, (2 specs.).

DISTRIBUTION (Fig. 12). Known only from the vicinity of Taizz, Yemen.

DESCRIPTION. Dextral; elongate conical; *ribs wavy, irregularly spaced and of varying thickness even within a single rib,* 2–3 ribs per mm. on body whorl; spiral striae absent; protoconch initially smooth, later with close, regular, sharp, straight ribbing. Sutures deep; narrow, shallow umbilicus; aperture sharp and unthickened. Colour pale brown, *with irregular, predominantly radial streaks or flammulations of opaque white.*

Shell. Dimensions of Holotype (Fig. 13e): 18·2 × 8·8 × 7·6; 7·7 × 5·5; 8·8 wh. The holotype is the largest of the four known specimens.

Anatomy. Unknown.

COMMENTS. Although the material is limited, it does show remarkable uniformity in shell form, and in view of the similar lack of conchological variability in the other small Arabian species of *Cerastus,* must be considered a valid taxon. Morphologically, the shell is closest to that of *girwanensis* from which it differs principally in the details of its ribbing and colouration.

Cerastus girwanensis Connolly, 1941

Cerastus girwanensis Connolly, 1941:27, pl. 3, fig. 13.

TYPE MATERIAL. Lectotype (here selected, BMNH 1939.4.19.9) and Paralectotype (BMNH 1939.4.19.10), Jebel Girwan, Yemen, 2700 m., leg. P. W. R. Petrie, 17.ii.1938.

DISTRIBUTION (Fig. 12). Known only from the type locality, Jebel Girwan, near Ghaiman, about 17 km SE. of Sana, Yemen.

DESCRIPTION. Dextral; elongate conic; apex blunt, sutures deep; protoconch initially smooth becoming ribbed, *ribbing regularly spaced, sharp and of even thickness (2–3 ribs/mm.),* spiral striae absent. Umbilicus narrow and shallow, aperture sharp, unthickened. Colour uniform pale brown, ribs paler.
    Shell. Dimensions of Lectotype (Fig. 13d): 17·0 × 9·5 × 8·0; 7·6 × 5·2; 7 wh.
    Anatomy. The radula and jaw of the smaller, immature, type were described by Connolly (1941:28); the radula closely resembles that of *C. scotti* but had considerably fewer teeth (Table 2). Like *scotti* the marginal ectocones were multicuspid in all but the first two teeth.

COMMENTS. See *C. albonotatus* above.

Cerastus scotti Connolly, 1941

Cerastus scotti Connolly, 1941:22, pl. 3, fig. 14, text fig. 7. [Jebel Jihaf].

TYPE MATERIAL. Holotype (BMNH 1939.4.19.11) and 6 paratypes (BMNH 1939.4.19.12–17), Jebel Jihaf, South Yemen, 2000–2300 m; 2 paratypes, Jebel Harir, South Yemen, BMNH, leg. Scott & Britton, x–xi. 1937.

OTHER MATERIAL. **Yemen:** Naqd Al Ahmar, between Ibb and Taizz, 2400 m., 25.ix.1977, leg Lavranos. **South Yemen:** Jebel Jihaf, 2000–2300 m., x–xi. 1937, leg. Scott & Britton, (4 specs.).

DISTRIBUTION (Fig. 12). Recorded from elevated sites in the region of Taizz, Yemen and Dhala, South Yemen, and it is thus more widely distributed than other small *Cerastus* species.

DESCRIPTION. Dextral; *elongate ovoid*; ribs fine, initally strong and regularly spaced, *becoming much weaker and less regular (6–9 ribs/mm.)*; weak spiral striae giving glossy surface appearance. Apex sharp, protoconch initially smooth; *sutures not deeply impressed*; narrow, shallow umbilicus; aperture sharp, unthickened. Colourless to very pale brown, semi-transparent; stronger early ribs may be translucent white.
    Shell. Dimensions of Lectotype (Fig. 13g): 19·3 × 10·6 × 9·1; 9·6 × 6·2; 6·9 wh.   Largest specimen: Naqd al Ahmar, Yemen: 22·7 × 11·1 × 9·8; 10·0 × 6·6; 8 wh.
    Anatomy. The jaw and radula were described by Connolly (1941:27, fig. 7); see Table 2. The remaining anatomy is unknown.

COMMENTS. *C. scotti* differs from the other small Arabian *Cerastua* by its shell shape and ribbing, resembling a small *C. schweinfurthi*. It is easily separated from the latter by its considerably smaller size for an equivalent number of whorls.

POLYCHORDIA Connolly, 1941

TYPE SPECIES. *Polychordia pulcherrima* Connolly [monotypy].

DIAGNOSIS. Shell as in *Crerastus* but more elongate with deeper sutures; costae thin and raised, regularly and widely spaced.

Polychordia pulcherrima Connolly, 1941

Polychordia pulcherrima Connolly, 1941:28, pl. 3, fig. 10.

TYPE MATERIAL. Holotype (BMNH 1939.4.19.55) and 10 paratypes (BMNH 1939.4.19.56–65), Wadi Thabad, north slope of Jebel Sabir, Yemen, c. 1800 m., 25–26.xii.1937, leg. Scott & Britton. 31 additional possible paratypes, as above, BMNH.

DISTRIBUTION (Fig. 12). Known only from the type locality at Jebel Sabir, near Taizz, Yemen.

DESCRIPTION. Dextral; elongate conical, apex blunt, sutures deep, whorls rather shouldered in profile, umbilicus narrow and shallow; protoconch initially smooth, becoming regularly ribbed, *ribs very prominent and sharp, regularly and widely spaced.* Aperture sharp, unthickened. Colour pale brown, translucent, ribs opaque white.

Shell. Dimensions of Holotype (Fig. 13f): $13·8 \times 5·2 \times 4·8$; $4·7 \times 3·3$; 8 wh. Largest paratype: $15·9 \times 5·8 \times 5·3$; $4·8 \times 3·3$; 8·1 wh.

Anatomy. Unknown.

COMMENTS. The shell is closest to that of *Cerastua girwanensis,* but differs in the strength and spacing of the ribbing. Connolly's original generic positioning is retained although it is probable that once the anatomy is known this species will be found to be a *Cerastus.*

EURYPTYXIS P. Fischer, 1883

TYPE SPECIES. *Pupa candida* Lamarck [monotypy].

DIAGNOSIS. Shell with clearly developed flared lip. Penis with short, rounded caecum; penial retractor with multiple insertion on penis and epiphallus in Arabian forms. Penial appendix with short, blunt papilla; appendicular retractor inserts at junction of basal and central portions of the appendix; base of central stalk not enclosed. Origin of penial and appendicular retractors separate or adjacent.

Euryptyxis candida (Lamarck, 1822)

?*Helix arabica* Forskal, 1775:127. [Loharjae], *nomen dubium.*
Helix sulcata Müller [*pars*]. Martini & Chemnitz, 1786:165, pl. 135, fig. 1231.
Pupa candida Lamarck, 1822:106. [loc. unknown]; 1833:171.
Buliminus forskalii Beck, 1837:68. [Arabia].
Pupa candida Lamarck. Delessert, 1847:pl. 27, figs 10a–b.
Buliminus forskalii Beck. Pfeiffer, 1842:45; Kuster & Pfeiffer, 1845–55: 49, pl. 15, figs 6, 7, pl. 18, figs 3, 4; Reeve, 1849:pl. LXI, species 419; Westerlund, 1887:64.
Pupa arata Récluz, 1843a:4; 1843b:pl. 75. [Socotra].
Bulimus fragosus Férussac. Reeve, 1849:pl. LXIV, species 446.
Bulimus candidus Deshayes. Férussac & Deshayes, 1851:77, pl. 150, figs 15, 16;
Buliminus candidus Lamarck. Rossmässler, 1880:41, pl. 198, fig. 1984; Westerlund, 1887:64.
Bulimus candidus Lamarck. Paladilhe, 1872:pl.1, fig. 17. Bourguignat, 1882: 16, figs 6–8.
Bulimus micraulaxus Bourguignat, 1882, 17, fig. 20. [Southern Arabia].
Buliminus eryx Westerlund, 1887:64. [Arabia].
Buliminus (Petraeus) eryx Westerlund. Rossmässler, 1888:31, pl. 99, fig. 559; Kobelt, 1902:402, pl. 71, figs 11, 12.
Buliminus (Petraeus) candidus Lamarck. Kobelt, 1902:407, pl. 72, figs 2, 3.
Euryptyxis forskalii Pfeiffer. Connolly, 1941:30; Verdcourt, 1974:8.
Pupa candida Lamarck. Mermod, 1951:717, fig. 71.
Euryptyxis candida Lamarck. Verdcourt, 1974:6; Mordan, 1980a: 360, fig. 2k.

TYPE MATERIAL. Possible Syntypes of *arata* Récluz, 'Yemen', Petit Collection, BMNH 1943.10.2.53–55, (3 specs.).

The Lamarck types of *candida* have not been examined but a representative specimen is well illustrated by Mermod (1951, Fig. 71), leaving no doubt as to the identity of the species. The name *Helix arabica* Forskäl predates *candida* but is here considered a *nomen dubium.* It is based

on material collected by Forskål himself which is now housed in the Copenhagen Museum (together with the material which forms the basis of the accounts of Martini and Chemnitz (1786) and Beck (1837)). The original description of *arabica* refers to a smooth, white shell ('*alba*' and '*glabra*'), whereas the specimens purporting to be the types are strongly ribbed (Fig. 16d) as in typical *candida*, and are mostly pale brown in colour. The description better fits *labiosa* Müller, and the true identity of *arabica* Forskål is clearly uncertain.

One specimen of *candida* from the Spengler collection, ZMC, is probably the original of a poor figure labelled *Helix sulcata* Müller in Martini and Chemnitz (1786, fig. 1231). This figure is cited as an indication by Beck (1837) for the name *Buliminus forskalii* and thus the Spengler specimen is most likely the type of *forskalii* Beck.

OTHER MATERIAL. **Yemen:** Ibb, leg. Haythornthwate, BMNH 1935.4.4.34, (1 spec.); 10 miles N. Zabid, leg. A. R. Waterson, 15.xii.1945, RSM 1953.52.105, (11 specs.); Wadi Rema, 1250 m., leg. A. R. Waterson, 2.ix.1946, RSM 1953.52.104, (2 specs.); Wadi Ja'ira, leg. A. R. Waterson, 4.ix.1946, RSM 1953.52.112, (4 specs); Wadi Hamman, 1700 m., leg. A. R. Waterson, 2.ix.1946, RSM 1953.52.107, (1 spec.); Wadi Thaban, N. side of Jebel Sabir, c 1850 m., leg H. Scott, BMNH 1939.19.43–45, (3 specs.); Wadi Dharh, NW. Sana, c 2500 m., leg. P. W. R. Petrie, vii.1938, BMNH, (4 specs.); 5 miles Taizz, leg. M. A. Brunt & J. D. Mather, xi.1971, BMNH, (2 specs); Wadi Zabid, leg. M. A. Brunt & J. D. Mather, BMNH, (8 specs.); 34 km. N. Taizz, leg. J. Lavranos, 1978, MNHN, (3 specs); As Saiyani, 32 km. N. Taizz, leg. M. Lavranos, 1977, MNHN, (1 spec.); Wadi Shadhb, 30 km. W. Menakha, 1400 m., leg. M. Lavranos, 1977, MNHN, (12 specs.); Al Maghriba, 2300 m, leg. M. Lavranos, 1977, MNHN, (2 specs); 20 miles N. Sana, Leg. M. Al-Safad, 1979, BMNH, (3 specs.); Taizz, 1400 m., Leg. P. Heath, iv.1978, BMNH 1982, (3 specs, 2 dissected); Al Hyma, near Taizz, 1100 m., Leg. P. Heath, ix. 1979, BMNH 1982, (3 specs, 2 dissected); Al Gharabi, Tihama, leg. M. D. Gallagher, 28.xi.1982, BMNH, (11 specs). **South Yemen:** near Dhala, leg. D. W. Bury, BMNH 1903.7.6.5–6, (2 specs.); Wadi Dareija, near Dhala, 1400 m., leg. H. Scott, BMNH 1939.4.19.19–20, (2 specs.); Dhala, over 1550 m., Leg. H. Scott, BMNH 1939.4.19.26, (1 spec.); Jebel Jihal, 1920–2200 m., leg. H. Scott, BMNH 1939.4.19.29–33, (5 specs.); Wadi Tiban, Musemir, leg. Petrie, BMNH 19407.13.24–26, (3 specs.). **Saudi Arabia:** East Cape, Dumsuk island, Farsan Islands, leg. W. A. Macfadyen, BMNH 1928.3.16.33–47, (15 specs.); Farsan Islands, leg. G. W. Young, BMNH 1931.4.25.83–84, (2 specs); Wadi Muhaishira, Jadaliya, leg. H. St. J. B. Philby, 17.i.1936, BMNH, (1 spec.); Suq Aiban, leg. H. St. J. B. Philby, 21.xii.1936, BMNH, (5 specs.); Math'an Plain, leg. H. St. J. B. Philby, 21.xii.1936, BMNH, (8 specs.); Wadi near Khamis Mishat, leg. A. R. Waterson, 24.viii.1944, BMNH 1945.8.23.187–190, (4 specs.); RSM 1953.52.115, (9 specs.); 10 miles N. Amk, Tihama, leg. A. R. Waterson, 14.ix.1944, RSM 1953.52.109, (4 specs.); Wadi Damat, Tihama, leg. A. R. Waterson, 14.iii.1945, RSM 1953.52.110, (1 spec.); ?Suda, leg. J. D. Toothill, BMNH 1952.10.30.55, (1 spec.); 65 km from Najran, on road to Abha, leg. J. Lavranos, 1980, MNHN (10 specs); Abu Arish, nr. Jizan, leg. Lavranos, 1980, MNHN (numerous); Wadi Manfar, Najran, leg. Lavranos, MNHN (1 spec.); Wadi Kharra, leg. K. Gotto Smith, 10.xi.1982, BMNH, (1 spec.).

DISTRIBUTION (Fig. 17). Restricted to the south-west of Arabia. The range is similar to that of *E. fragosa,* but extends further northwards into the Asir province of Saudi Arabia, and westwards to the Farsan Islands in the Red sea. The southern- and eastern-most localities are respectively near Musaymir and in the region of Dhala, both in South Yemen. A number of early records are from Socotra, but these have not been confirmed in recent years.

DESCRIPTION. Dextral; pupiform, surface with strong sharp *regular radial ribs,* and very fine, wavy spiral striae which cross the ribbing; protoconch initially smooth becoming radially ribbed; umbilicus closed. Aperture with *flared lip, never recurved,* and often thickened just internal to the margin; *strong internal columellar fold in body whorl* (Fig. 18D), not visible from aperture. Colourless opaque to brown, lip may be more deeply pigmented.

Shell. Dimensions of figured syntype *candida* Lamarck (Mermod, 1951:717, fig. 71): shell height 24·5; shell diam. 13·0; apert. height 12·0; whorls 7·5.   Syntypes *arata* Récluz: 25·9 × 13·4 × 12·1; 12·9 × 9·4; lip 1·9; 7·7 wh.; 25·4 × 13·1 × 11·9; 13·2 × 10·1; lip 1·8; 7·6 wh.;   25·7 × 13·5 × 11·2; 13·1 × 9·4; lip 2·1; 7·7 wh. Largest specimen, Dhala, South Yemen, leg H. Scott (Fig. 16a): 40·1 × 19·9 × 16·1; 18·5 × 14·0; lip 3·4; 8·9 wh.   Smallest specimen, Dumsuk Island, Red Sea, leg Macfadyen (Fig. 16c): 16·8 × 10·0 × 8·2; 9·8 × 6·2; lip 1·0; 6·4 wh.
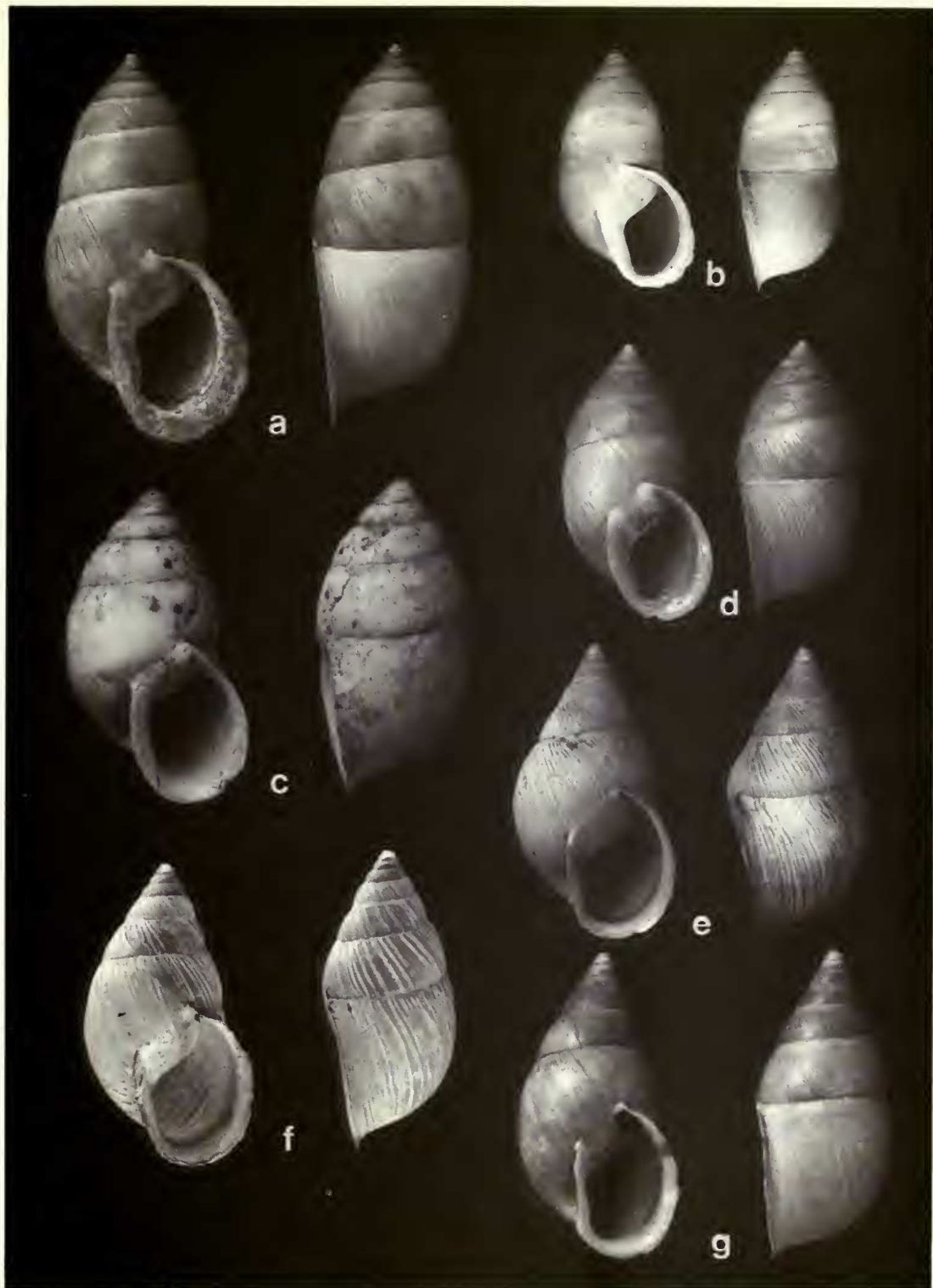
Fig. 16 *Euryptyxis candida:* a, Dhala, S. Yemen, BMNH 1939.4.19.26, × 1·5; b, Khamis Mishat, Saudi Arabia, BMNH 1945.8.23.187, × 1·5; c, Dumsuk Islands, Red Sea, BMNH 1928.3.16.33, × 3; d, possible type of *Pupa arabica* Forskal, ZMC, × 1·5; *Euryptyxis fragosa:* e. Hauban, RSM 1953.52.111, × 1·5; f, between Karia and al Seiyani, Yemen, MNHN, × 1·5; g, specimen ex Beck Collection, ZMC, × 1·5.
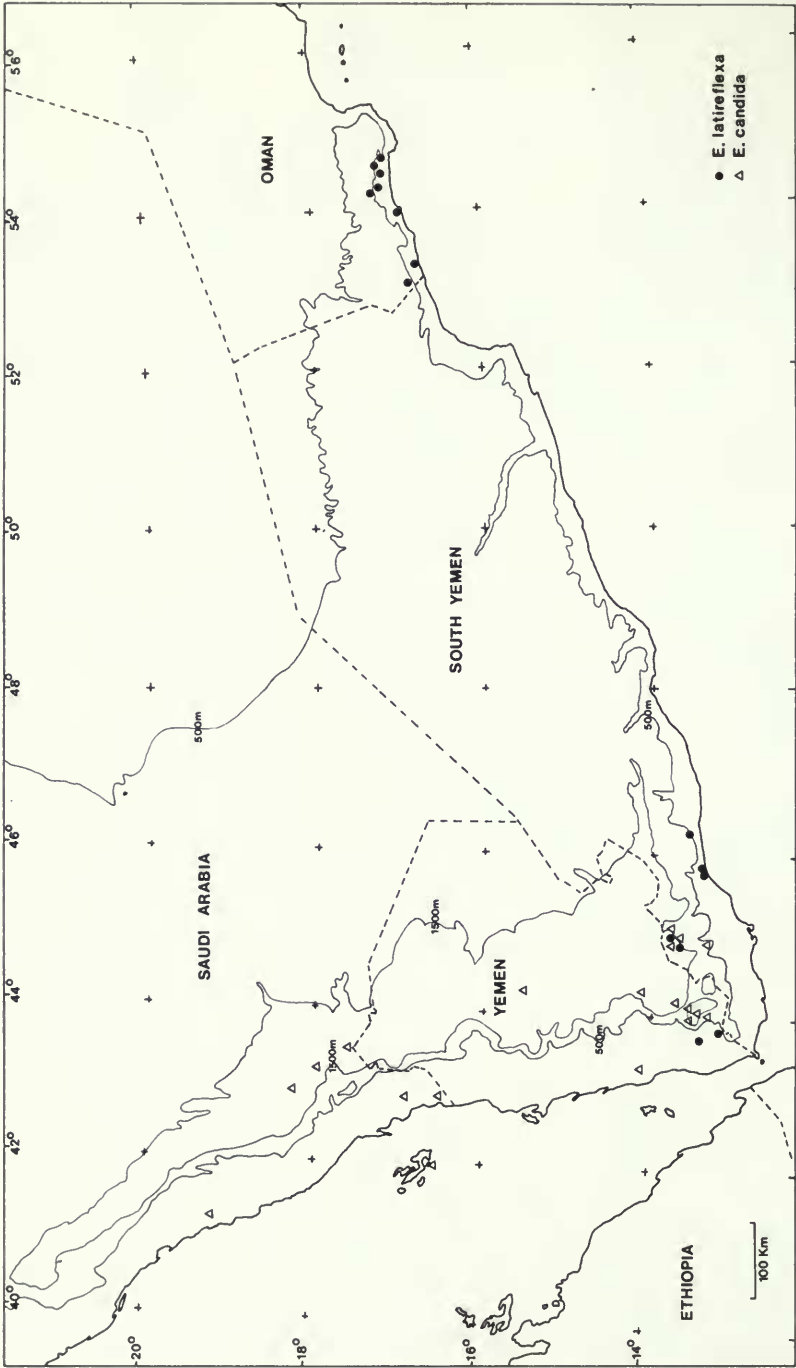
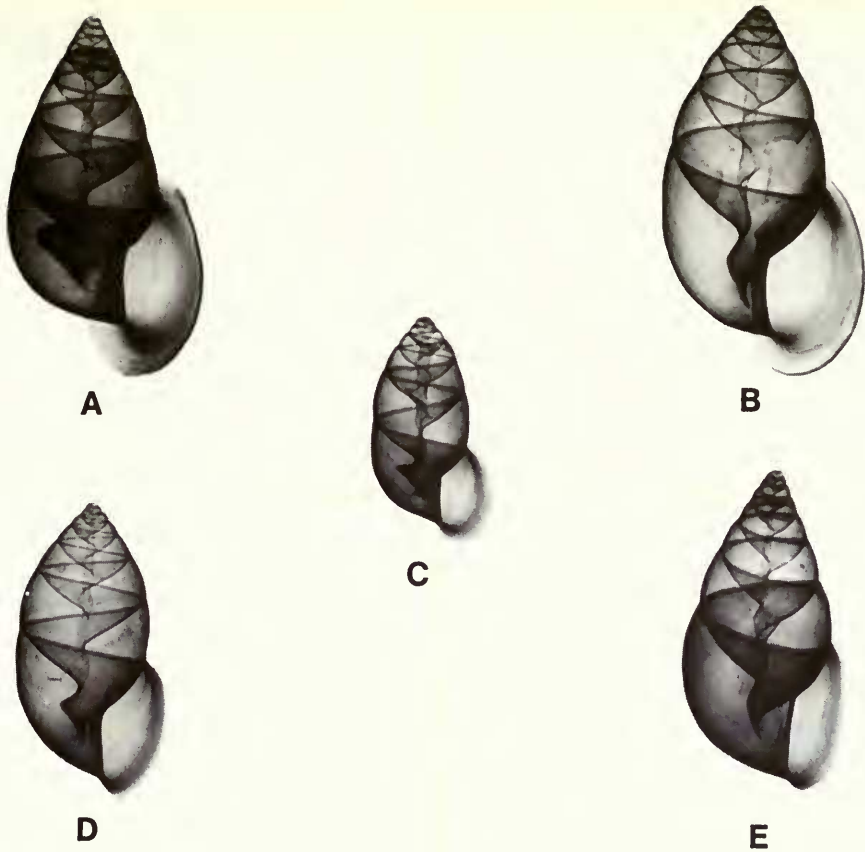**Fig. 17**   Distribution map of *Euryptyxis candida* and *latireflexa*.

Fig. 18 X-ray photograph of *Euryptyxis* species to show relative development of the columellar fold;
A, *latireflexa;* B, *revoili;* C, *labiosa;* D, *candida;* E, *fragosa;* × 1·4.

In fresh specimens the protoconch and early whorls are always a rich, glossy brown, typically becoming progressively paler until the shell becomes a milky transluscent grey/white. Occasionally the entire shell retains the brown colouration. In most specimens the internal lip surface has a brown rim, well illustrated by Delessert (1847, pl. 27, fig. 10).

Sculpture does not in general appear to vary greatly, with the sharp, regular radial striae always predominating. There is, however, a considerable range in size and, to a lesser extent, shape, although the latter is always characteristically pupiform. Material from coastal sites such as Jizan and Dumsuk Island are remarkable for their small size, and a more-elongate shape (the *forskali* form) appears to be characteristic of shells from the upland region of Asir in Saudi Arabia.

Body. Taizz specimens of a uniform cream colouration, with slightly darker pigmentation on tubercles of head.

Radula (Figs 19a–b). Total number of teeth per row in *candida* from Taizz between 40–42 (Table 2), although Hesse (1933) quoted a figure of 50 teeth for Menaha material. Central and lateral ectocones clearly developed but small. Mesocone of marginals rounded and ectocones bear single, wide pointed cusp; in some most marginal teeth ectocone becomes bicuspid.

Lung cavity. As in *E. latireflexa* (see below), with kidney extending 0·75–0·8 times cavity length. Outer lung wall weakly pigmented with brown and white streaks close to mantle collar.

Reproductive system. (Figs 20, 21). Hermaphrodite gland composed of 4 to 5 diffuse lobes, loosely imbedded in digestive gland and lying against parietal and columellar shell walls.
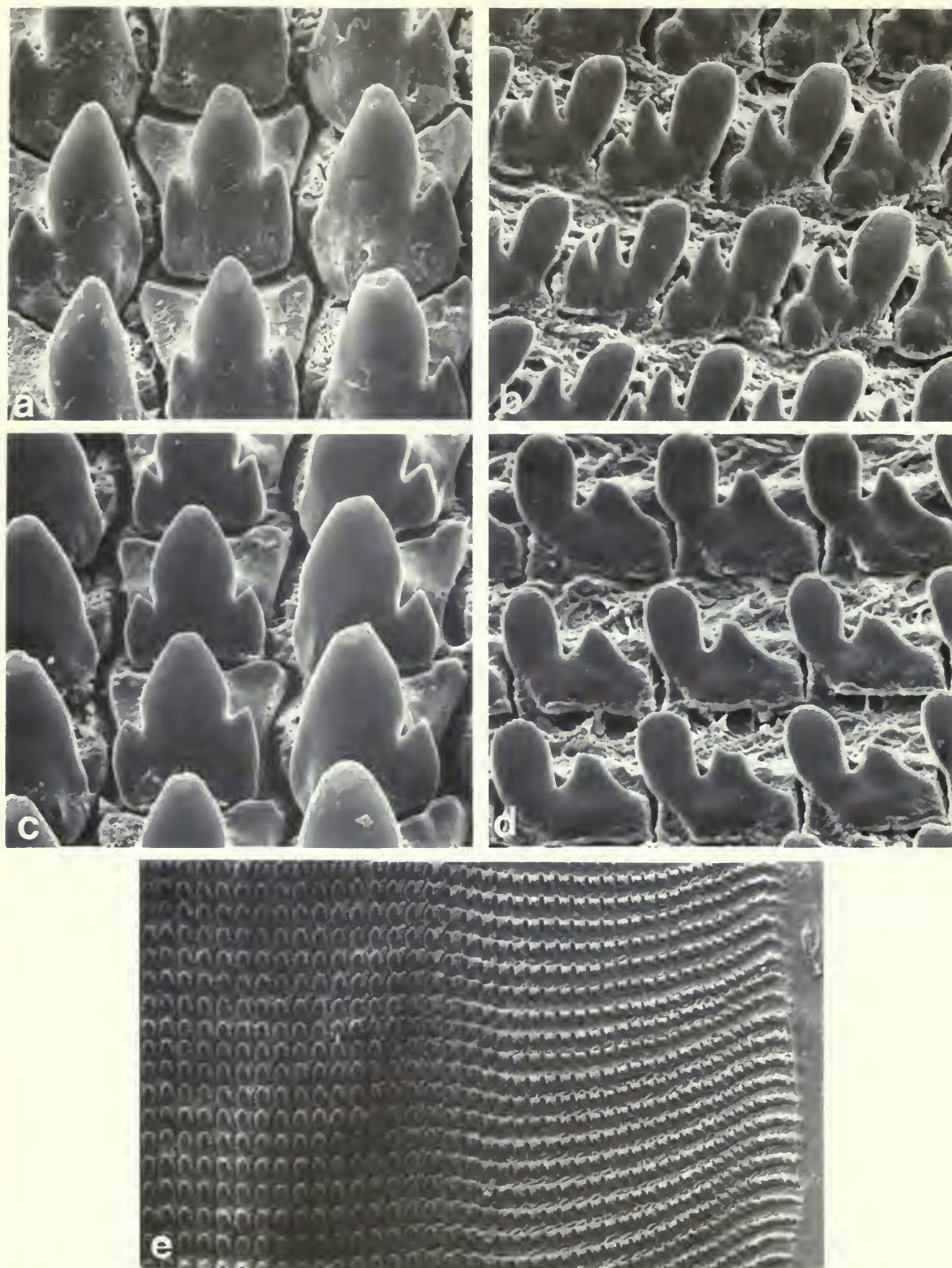
Fig. 19 Radular teeth of *Euryptyxis:* a, *E. candida,* Taizz, Yemen, 1979, central and lateral teeth; b, marginal teeth; c, *E. fragosa,* Taizz, Yemen, 1979, central and lateral teeth; d, marginal teeth; × 720; e, entire side of radula; × 80.
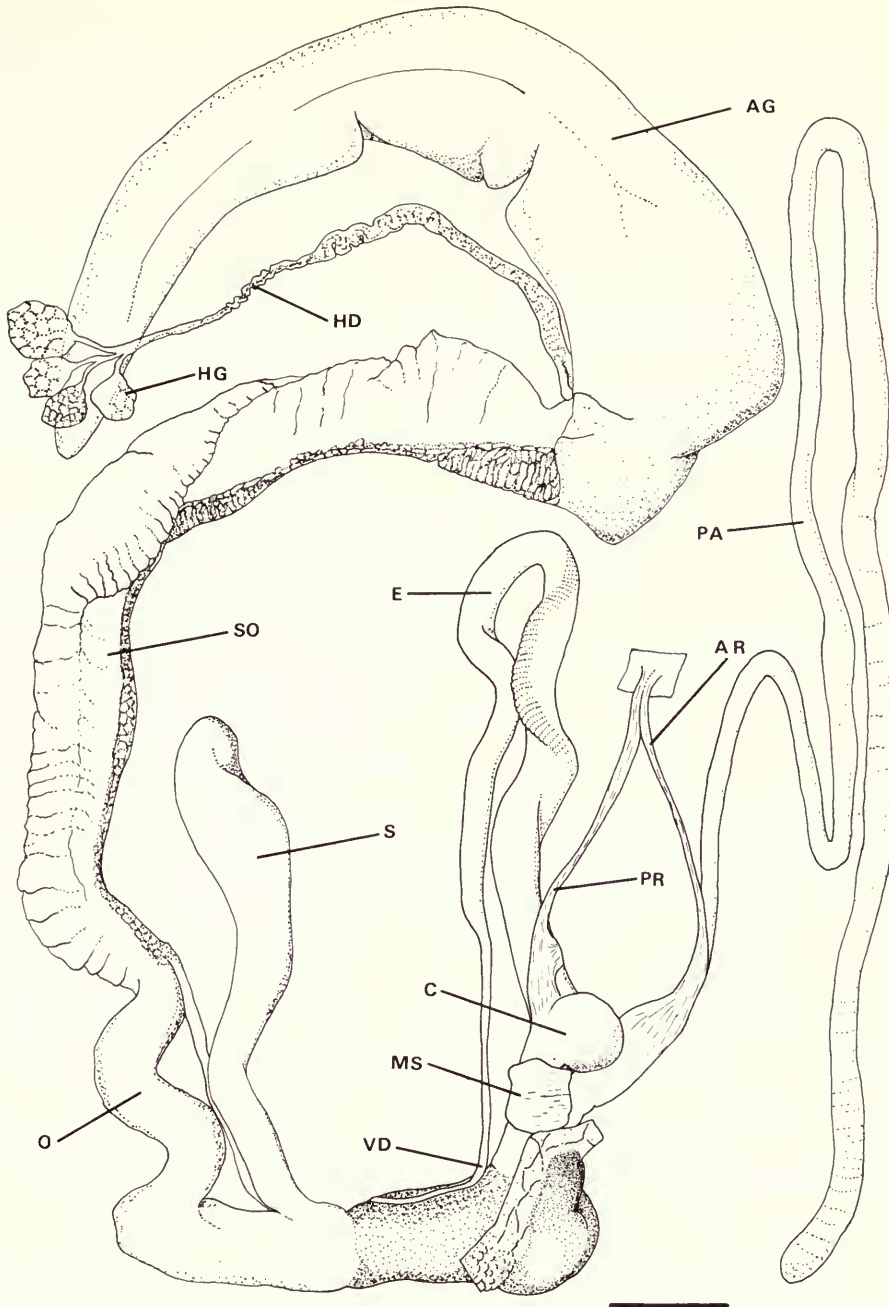
Fig. 20 Genital system of *Euryptyxis candida*, Taizz, 1979. Scale 2 mm.

Hermaphrodite duct long and thin, with elongate seminal vesicle (*sensu* Bayne, 1973) which is only weakly convoluted; talon simple fold in duct (Fig. 21B). Albumen gland relatively large for genus, 1·1–1·3 times length of spermoviduct.

Free oviduct about three times length of vagina, continuous with the atrium and darkly pigmented almost throughout its length; both attached to body wall by numerous short muscles.

Fig. 21   *Euryptyxis candida,* Taizz, 1978: A, epiphallus; B, talon region; C, penis. Scale 1 mm.

Atrial retractor fairly strong, branching from main columellar muscle. Internally free oviduct bears weak, irregular longitudinal pillasters. Spermatheca approximately same length as free oviduct and not obviously separable into distinct head and stalk regions. Terminal portion of vas deferens differentiated into long epiphallus, about five times length of penis; exter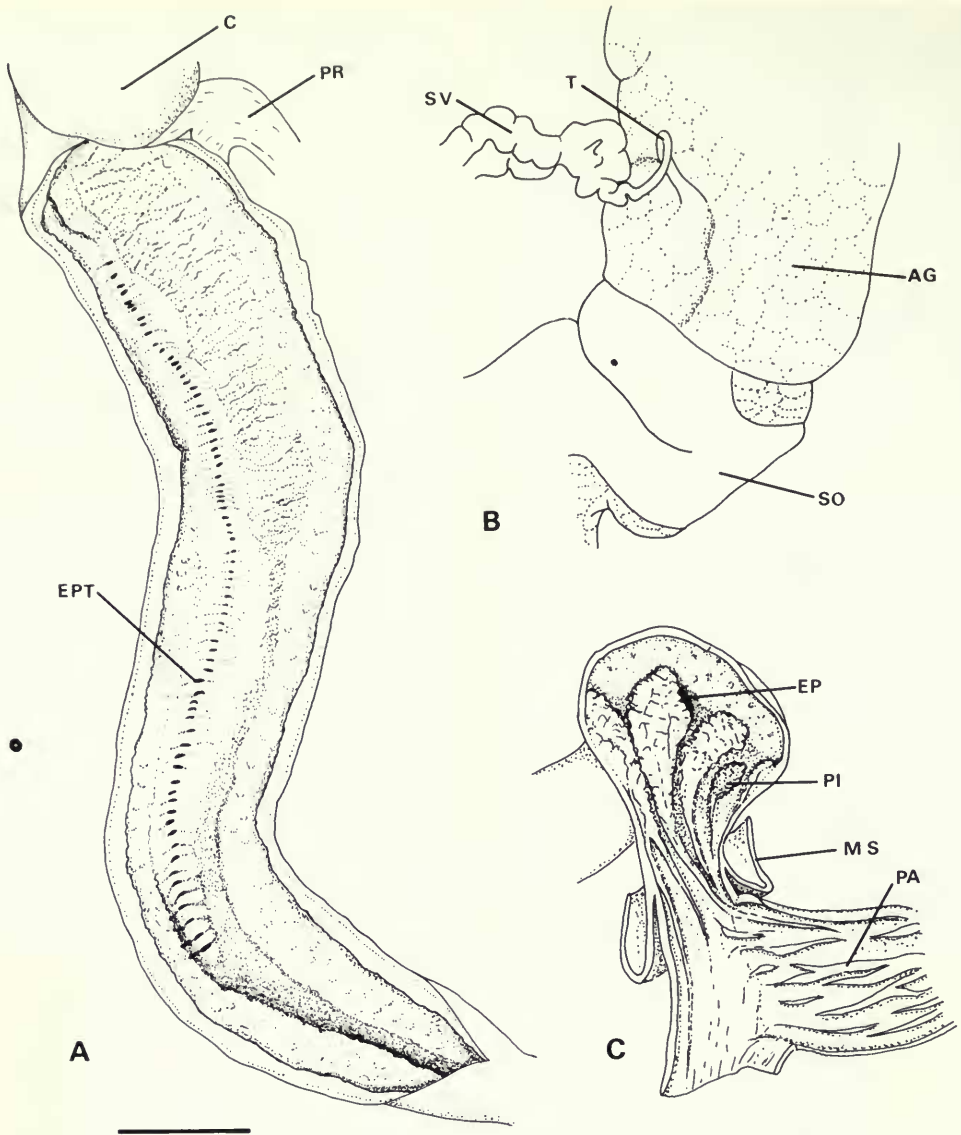nally with longitudinal row of transverse ridges, corresponding to line of internal pits, varying in number between 75 and 77 in the Taizz material (Fig. 21A). Epiphallus enters penis just below caecum.

Penis characterised externally by large, bulbous, thin-walled caecum at top; caecum may be globular or pointed. Penis small relative to other *Euryptyxis,* and has muscular collar or sheath, attached above and recurved at base to form two-layered structure (Fig. 21C). Internally are four principal glandular areas, three large and one very much smaller, which continue downwards as tapering pilasters. Pattern asymmetrical: two large glandular patches, which appear almost fused,

lie to one side of epiphallar pore, with remaining large and small areas quite distinct on other side, overlying point of entry of the appendix at base of penis. Appendix clearly divisible into three distinct regions: a short, wide basal portion, internally lined with reticulum of predominantly longitudinal pilasters; a long, thin, thick-walled central portion with a narrow lumen; and a wider, terminal saculate portion of similar length but with very thin, transparent wall. Penis and appendicular retractor muscles originate together about one third way up lower lung wall; may initially be fused over a short distance. Penis retractor bifurcates prior to insertion, one branch inserting transversely at penis/epiphallus junction, other laterally just above, on epiphallus proper.

COMMENTS. Although *candida* exhibits enormous variation in size, the shape and sculpture of the shell are relatively constant, and it is significant that all smaller specimens are from coastal locations. Its pupiform shell shape and strong, regular radial ribbing combined with aflared but unreflexed lip distinguish it from other *Euryptyxis*.

Reproductive anatomy is most similar to *E. fragosa,* but at Taizz, Yemen where both are sympatric, there are differences in the epiphallus and penial appendix.

Euryptyxis fragosa (Pfeiffer, 1842)

Bulimus fragosa Férussac, 1821–2:59. [Les Grandes Indes], *nomen nudum*.
Buliminus fragrosus Férussac. Beck, 1837:68. *nomen nudum*.
Bulimus fragosus Férussac. Pfeiffer, 1842:45. [Yemen].
Bulimus fragosus Férussac. Küster & Pfeiffer, 1845–55:62, pl. 18, figs 1, 2; Bourguignat, 1882:14, fig. 19.
Buliminus fragosus Férussac. Rossmässler, 1880:41, pl. 198, fig. 1983.
Buliminus fragosus Pfeiffer. Westerlund, 1887:64.
Buliminus (Petraeus) fragosus Férussac. Kobelt, 1902:406, pl. 172, fig. 1.
Euryptyxis fragosa Pfeiffer. Connolly, 1941:30.
Euryptyxis fragosus Pfeiffer. Fisher-Piette & Métivier, 1972:1293.

TYPE MATERIAL. Férussac's original naming of this species was invalid, the first comprehensive description being given by Pfeiffer (1842). However, Pfeiffer's original material has not been traced and may possibly have been lost with the destruction of the Dohrn Collection in the Stettin Museum during the 1839–45 war (Dance, 1966:285). Two shells labelled *Helix fragosa* Fér. were found in the Férussac collection in Paris but these are *E. candida*.

OTHER MATERIAL. **Yemen:** El Kubar, leg. G. W. Berry, BMNH 1908.2.21.3, (1 spec.); Wadi Dhulla, 5 miles NW. Sana, c. 2500 m., leg. P. W. R. Petrie, vii.1938, BMNH, (26 specs.); Taizz district, 1250–1550 m., BMNH 1939.4.19.18, (1 spec.); Hauban, nr. Taizz, leg. A. R. Waterson, 7.viii.1946, RSM 1953.52.111, (7 specs.); 30 miles S. Taizz, 1250 m. leg. A. R. Waterson, 13.xii.1945, RSM 1953.52.114, (5 specs.); near Taizz, leg. A. R. Waterson, 8.iii.1946, BMHN 1948.9.7.4–13, (10 specs., 3 dissected); near Taizz, 1250 m., leg. A. R. Waterson, 13.xii.1946, RSM 1953.52.102, (3 specs,); Between Rahida and Taizz, leg. A. R. Waterson, 7.xii.1945, RSM 1953.52.113, (22 specs); 5 miles from Taizz, leg. M. R. Brunt and J. D. Mather, xi.1973, BMNH, (3 specs.); Al Seiyani, 32 km. N. Taizz, leg. M. Lavranos, 1977, MNHN, (2 specs.); Wadi Shadbh, 35 km W. Menakha, 1400 m, leg J. Lavranos, 1977, MNHN (2 specs); Al Maghriba, 5 km W. Menakha, leg. J Lavranos, 1977, MNHN (5 specs); Between Karia and Al Seiyani, 1600 m., leg. M. Lavranos, 1979, MNHN, (8 specs.); Hamman Ali, leg. M. Lavranos, 1978, MNHN, (5 specs.); Qubesh, 1700 m., leg. M. Lavranos, 1979, MNHN, (2 specs.); Taizz, 1400 m, leg. P. Heath, iv. 1978, BMNH 1982, (2 specs., 2 dissected); Al Hyma, near Taizz, 1100 m., leg. P. Heath, ix.1979, BMNH 1982, (4 specs., 3 dissected); **South Yemen:** Wadi Leje, Jebel Jihaf, leg. H. Scott, BMNH 1939.4.19.1–8, (7 specs.); Jebel Jihaf, 1200 m., leg. H. Scott, BMNH 1939.4.19.21–24, (4 specs., 2 dissected); Jebel Jihaf, 1950–2050 m., Leg. H. Scott, BMNH 1939.4.19.25, (1 registered spec., 14 further unregistered specs.); Dhala, 1500 m., leg. H. Scott, 12–14.ix.1937, BMNH, (4 specs.); Mukieras, leg. G. Lancaster Harding, 1958, (11 specs).

DISTRIBUTION (Fig. 22). The most restricted of the four recognised Arabian *Euryptyxis* species. Almost all of the material examined here was collected in and around Taizz, although conchologically similar material has been recorded as far north as Manakha. The relatively smooth, slender form was found abundantly at Jebel Jihaf, near Dahla in in South Yemen, but also near Hamman Ali, between Yarim and Sana'a.
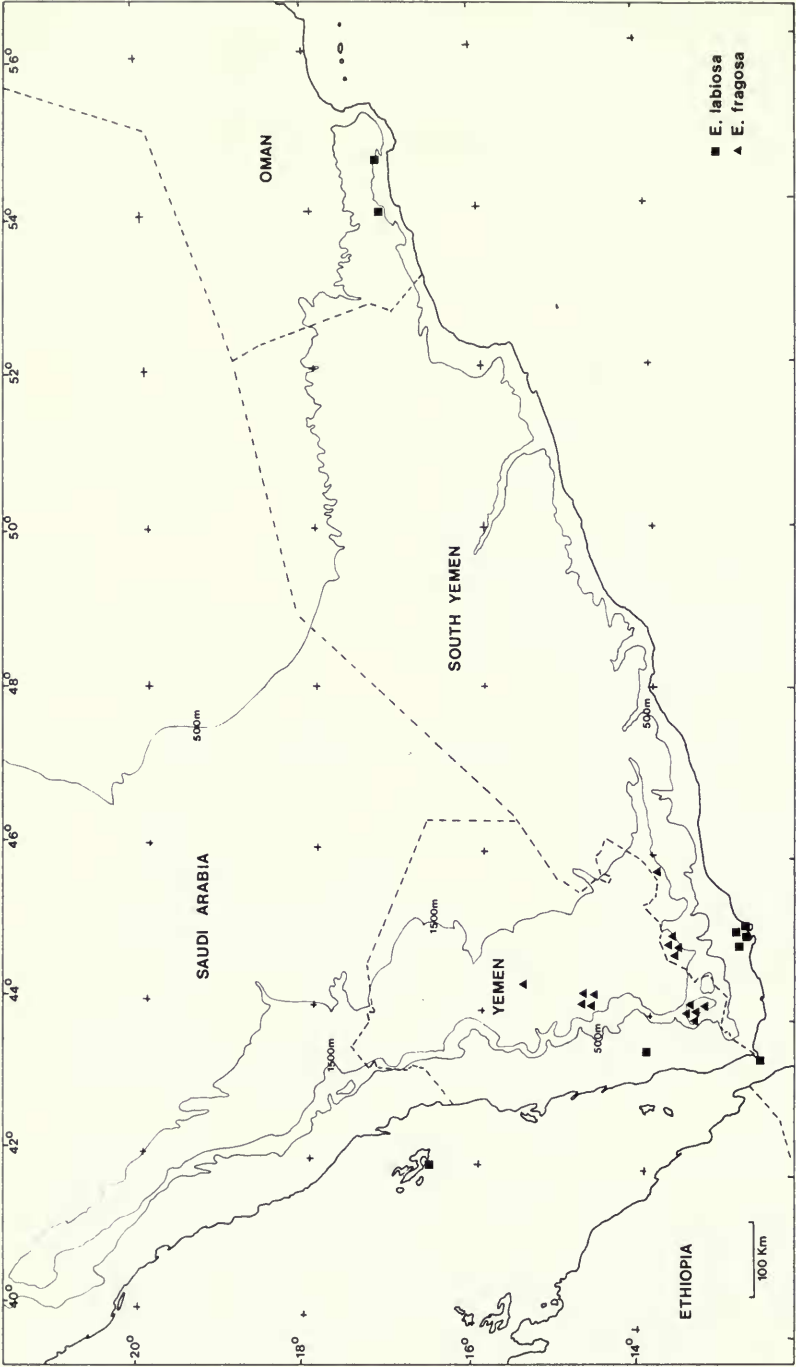
Fig. 22   Distribution map of *Euryptyxis labiosa* and *fragosa*.

DESCRIPTION. Dextral, *rounded elongate conical;* surface with regular radial ribbing varying from coarse to very fine, *becoming less evenly spaced, wavy, and usually weaker towards the aperture,* and fine wavy spiral striae; protoconch smooth, becoming ribbed; umbilicus closed. Aperture with *flared lip, never recurved; no internal columellar tooth* (Fig. 18E). Colour opaque white, rarely greyish brown with white ribs.

Shell. Dimensions: Taizz, Yemen, leg. Waterson, 1946: 30·0 × 15·1 × 13·3; 14·2 × 10·0; lip 1·6; 8·7 wh. Taizz, Yemen, leg. Heath, 1979: 35·8 × 19·1 × 16·6; 19·1 × 13·7; lip 2·9; 8·6 wh. Jebel Jihaf, South Yemen, leg. Scott: 28·8 × 15·0 × 12·7; 14·5 × 10·0; lip 1·3, 8·2 wh.

The principal sculptural variation is found in the radial ribbing which may be very strong (Fig. 16F), as in some populations around Taizz, or almost absent (Jebel Jihaf); other populations in the Taizz region have intermediate sculpture. Coarse ribbing appears in general to be correlated with a rather wider shell than normal, whereas the smoother shells are more slender in profile; individual populations show little variation in either respect.

Body. Uniformly pale cream, with slight dark pigmentation on tubercles in head region.

Radula (Figs. 19c–e). Very similar to *E. candida* (see Table 2).

Lung cavity. Typical for genus (see *E. latireflexa* below), but kidney relatively shorter than other species, occupying 0·7 times lung length (Table 3). Outer wall of lung unpigmented.

Reproductive system (Figs 23, 24). Albumen gland relatively short and narrow, approximately 1/3 length of spermoviduct. Spermatheca about 1·5 times as long as free oviduct; in one specimen it contained fragments of a partly dissolved spermatophore: tail region complete and shaped much as in *Zebrinops*; one complete digitiform spine also present (Figs. 24C–D).

Epiphallus thick, externally bears strong transverse ridges corresponding internally to longitudinal row of 40 to 57 pits (Figs. 24A). Penis with globular caecum (smaller than in *E. candida*) and sharply recurved muscular sheath. Penis and appendicular retractor muscles originating separately but at same leve on lung wall; former has multiple insertion on epiphallus, and main branch to penis. Internally, penis with rather variable pilaster pattern. Within individual Taizz populations, overall distribution of glandular patches and pilasters similar, but differences present in degree to which the two lateral glandular areas embraced epiphallar pore, and also in separation of these from their downward extensions by the transverse groove. Also differences in number, strength and regularity of pilasters in base of penial appendix.

Penial appendix characterised by thickening of basal region of central stalk (Fig. 23), unlike other Arabian *Euryptyxis*; thickening more marked in Taizz specimens than in those from Jebel Jihaf, but clearly developed in latter. Insertion of appendicular retractor muscle normal for genus.

COMMENTS. Despite considerable inter-population variation in shell sculpture and shape, specimens from three populations from Taizz showed a close degree of similarity in their anatomy. The sample from Jebel Jihaf, whilst being much smoother and more slender than any of the Taizz examples, was anatomically similar, and the number of epiphallar pits (48–49) was within the range shown by the Taizz material (40–57) (Table 5).

The species is characterised both by the number of epiphallar pits and the enlarged base of the central part of the penial appendix. All the forms agree in having a generally conical outline to the shell (as opposed to the pupiform shape of *candida*), a lip which is flared but never reflexed, a very weakly developed columellar fold, and distinct, regular spiral striae. These conchological similarities, in conjunction with the overall anatomical similarities, suggest that in the present state of knowledge all the forms should be included within a single species.

Eurypyxis labiosa (Müller, 1774)

Helix labiosa Müller, 1774:96. [In India].
Helix arabica Forskal, 1775:127. [Loharjae].
Helix cylindracea acuta Martini & Chemnitz, 1786:166, pl. 135, fig. 1234. [*nomen nudum*].
Helix labiosa Müller. Gmelin, 1791:3645; Dillwyn, 1817:347.
Bulimus labiosus Bruguière, 1792:347.
Buliminus labiosa Müller. Beck, 1837:69.
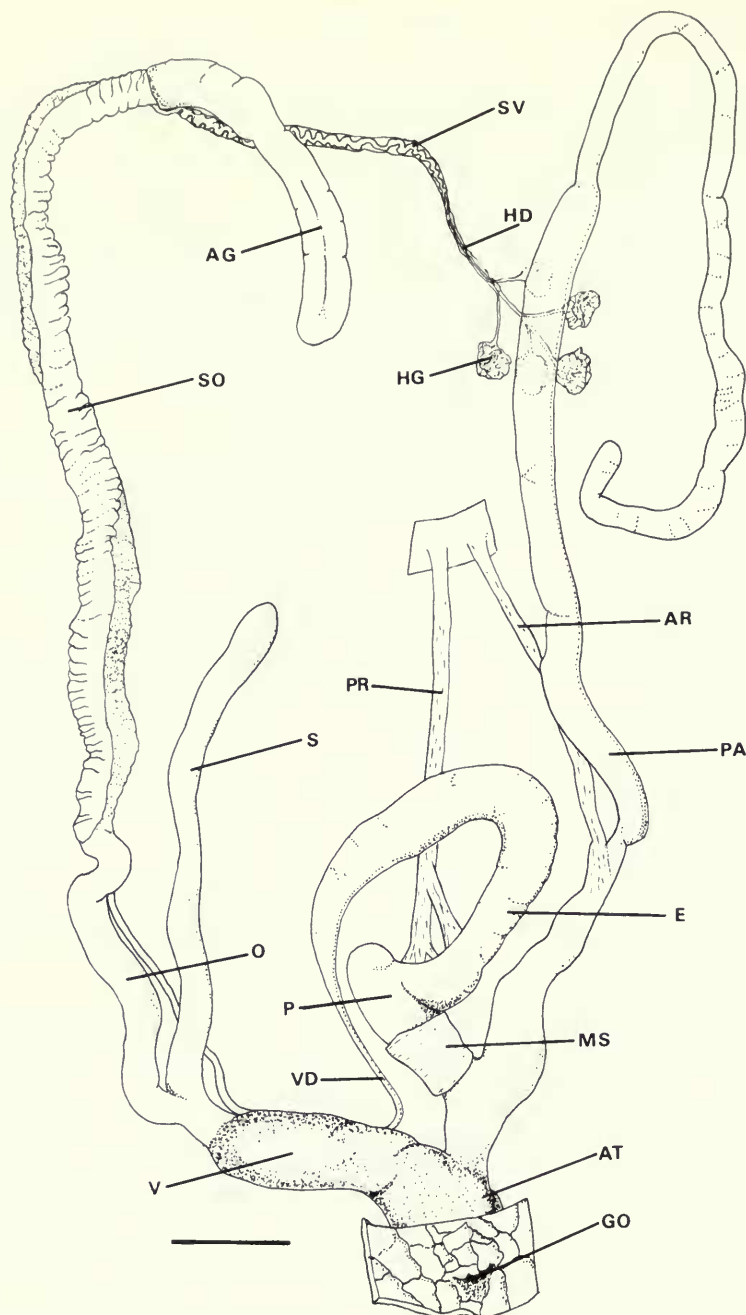
Fig. 23   Genital system of *Euryptyxis fragosa,* Taizz, Yemen, 1979. Scale 2 mm.

Pupa jehennei Récluz, 1843a:4; 1843b:pl. 76. [Socotra].
Bulimus labiosus Müller. Küster & Pfeiffer, 1845–55:48, pl. 15, figs 1, 2; Pfeiffer, 1848:67; Reeve, 1849:
     pl. LX, species 412; Bourguignat, 1882:20, fig. 11.
?*Bulimus bruguieri* Bourguignat, 1882:25. [? loc.].
Buliminus labiosus Müller. von Martens, 1889:149.
Buliminus (Petraeus) labiosus Müller. Rossmässler, 1893:84, pl. 171, fig. 1107.
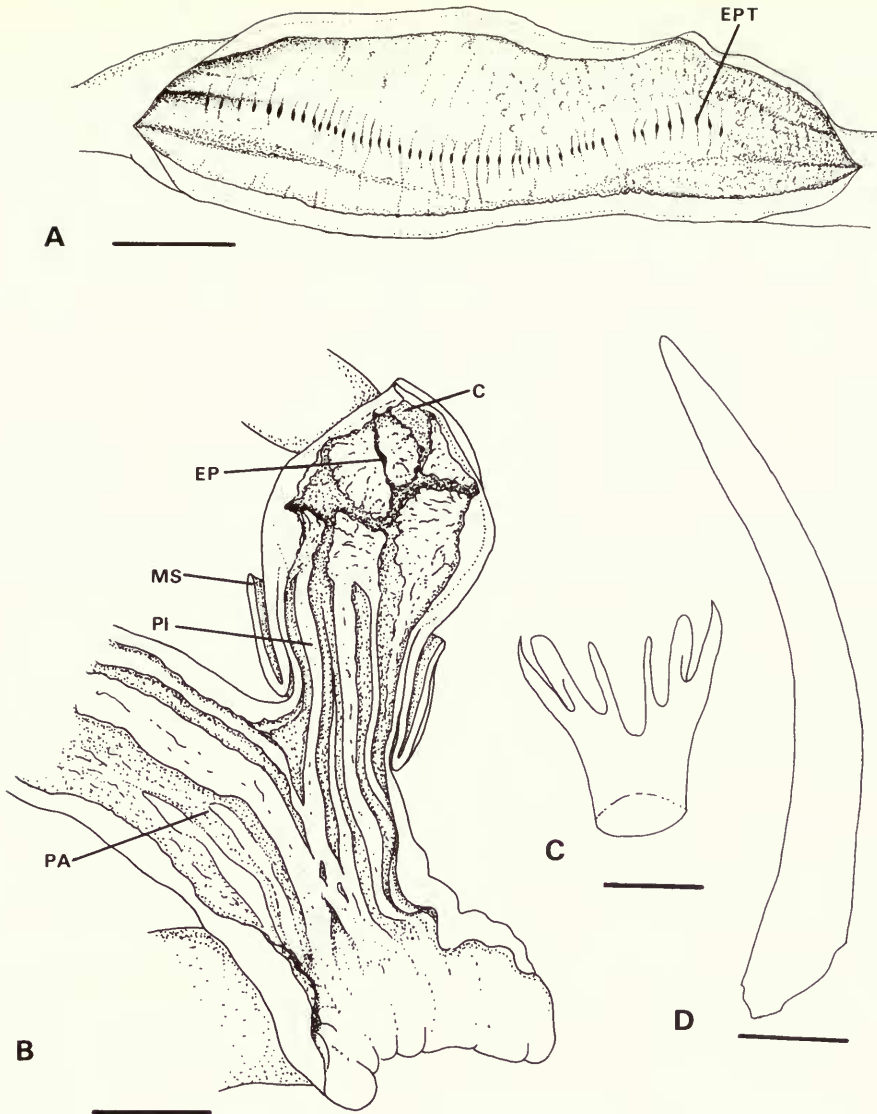
Fig. 24   *Euryptyxis fragosa,* Taizz, Yemen, 1979: A, epiphallus, scale 1 mm; B, penis, scale 1 mm; C, spermatophore spine, scale 0·2 mm; D, spermatophore tip, scale 0·5 mm.

Bulimulus hypodon Pilsbry, 1897:102. [Lower California].
Euryptyxis labiosus jehennei Petit. Pilsbry, 1897–8:156, p121, figs 5–7
Buliminus (Petraeocerastus) labiosus Müller, Kobelt, 1902:890, pl. 127, figs 6–9.
Euryptyxis labiosa Müller. Mordan, 1980a:360, fig. 2k; 1980b:106, pl. 2.

TYPE MATERIAL. Possible Syntype of *jehennei* Récluz, Petit Collection, BMNH 1843.11.27.88.   Holotype of *hypodon* Pilsbry, California *sic,* ANS.

The material described by Müller in his *Vermium terrestrium et fluviatilum* . . . of 1774 is housed in the Zoological Museum, Copenhagen but I have been unable to trace the types of *labiosa* there. Although the original description of *labiosa* is arguably ambiguous in the absence of types, the subsequent usage of the Müller's name is clear and his authorship is retained. Pilsbry's naming of *hypodon* clearly arose from an erroneous locality.

Table 5   Numbers of pits in the epiphallus of *Euryptyxis* species

Species	Locality	no. specs.	no. pits.
E. candida	Taizz, Yemen, 1978	2	76–77
	Taizz, Yemen, 1979 £	2	75–77
E. latireflexa	Dahaq Thu'ari, Dhofar, 1940	2	19–20
	Khadrafi, Dhofar, 1976	3	17–23
	Ain Arzat, Dhofar, 1976	10	17–26
	Tawai Atair, Dhofar, 1978 $	2	19–28
	Salalah, Dhofar, 1981	1	24
E. fragosa	Taizz, Yemen, 1946	3	40–42
	Jebel Jihaf, S. Yemen, 1938	2	48–49
	Taizz, Yemen, 1979 £	2	52–53
E. labiosa	Tawai Atair, Dhofar, 1981 $	2	30–32
E. revoili	Nogal, Somalia, 1961	2	24–25

£, $ Syntopic species pairs.

OTHER MATERIAL. **Yemen:** Menaka, leg. Schweinfurth, BMNH 1895.8.20.3, (1 spec.); Senna [? = Sana, Wadi Hadramaut, c 500 m], leg. Preston, 5.x.1903, BMNH, (3 specs); Senna, RSM 1961.61, Salisbury Colln., (1 spec.); 6 miles W. of Heis, leg. A. R. Waterson, 13.xii.1945, RSM 1953.52.117, (6 specs). **South Yemen:** Aden, leg. A. E. Craven, vii.1877, BMNH 1880.10.1–2, (2 specs.); leg. A. W. Baynham, BMNH 1885.8.9.12–14, (3 specs); leg. Yerbury, BMNH 1888.4.9.354, (1 spec.); leg. Shopland, BMNH 1902.5.14.1–5, (5 specs.); leg. W. Blume, BMNH 1937.12.30.2215, (1 spec); leg. Shopland, 1937.12.30.2216–17, (2 specs.); leg. Lander, BMNH, (13 specs); Gold Mohur Valley, Aden, leg. A. J. Piele, RSM 1961.61, (7 specs.); Perim Island, leg. J. J. Walker, BMNH 1891.1.31.189–91, (3 specs, and 2 unregistered). **Saudi Arabia:** Dumsuk Island, Farsan Islands, leg. W. Macfadyen, BMNH 1928.3.16.29–32, (4 specs.); BMNH 1937.12.30.2225–32, (8 specs); Habile, leg. J. Lavranos, 1980, BMNH (5 specs); **Oman:** Dhofar, Leg. Mrs J. T. Bent, 1894–5, BMNH 1898.12.4.21–3, (3 specs.); Tawi Atair, Jabal Samhan, leg. M. D. Gallagher, 9.iv.1977, BMNH, (5 specs.); leg. M. D. Gallagher, 30.iv.1978, (17 specs., 3 spirit, 2 dissected); leg. J. N. Barnes, 15.iii.1980, BMNH, (6 specs.); between Ayub and Teetam, Jabal Qara, 800 m., leg. M. D. Gallagher, 31.viii.1982, BMNH, (3 specs.).

DISTRIBUTION (Fig. 22). It is difficult to assess the precise range of this species, which could occur almost continuously from Dhofar to the south-eastern coast of the Red Sea, although almost all the material considered here is either from localities in Dhofar, or the environs of Aden where the snail seems to be particularly abundant. Odd specimens from the Hadramaut [Preston], and the Tihama of Yemen [Waterson] and Saudi Arabia [Lavranos] do, however, suggest such continuity. In addition to the continental distribution, *labiosa* has been recorded from the Farsan and Perim Islands in the Red Sea, as well as Socotra (the type locality of *jehennei*), Cape Gardafui, Somalia (Bourguignat, 1882:31), and one doubtful record from the Seychelles. All records are from sites at comparatively low elevations, the highest being 800 m in Dhofar.

DESCRIPTION. Dextral, *elongate pupiform,* surface with regular radial ribs becoming weaker and more widely spaced towards aperture, and fine wavy spiral striae; protoconch smooth becoming strongly ribbed; umbilicus closed. Aperture with *recurved lip, and strong internal columellar tooth* (Fig. 18C). Colour usually transparent or opaque white, may be tinged with brown; lip white.

Shell. Dimensions of syntype *jehenni* Récluz: 25·1 × 12·0 × 9·2; 12·1 × 9·3; lip 2·5; 8 wh.   Holotype of *hypodon* Pilsbry (Fig. 25e): 25 × 12·5; 13·0 × 10·2; lip 2·3; 7·5 wh.   Largest specimen, Aden, leg. Baynham: 23·9 × 11·5 × 9·3;   11·5 × 9·1; lip 2·2;   7·3 wh.   Tawai Atair, Dhofar. leg. Gallahagher: largest: 21·4 × 10·8 × 9·3; 9·9 × 8·7; lip 1·5; 7·2 wh.   Smallest: 15·9 × 8·9 × 8·1; 7·8 × 6·0; lip 1·0; 6·2 wh.   This

Shell shape varies considerably within the species, even within samples from a single site. This is exemplified by the results of a statistical comparison of three 'age classes' of shells: living,
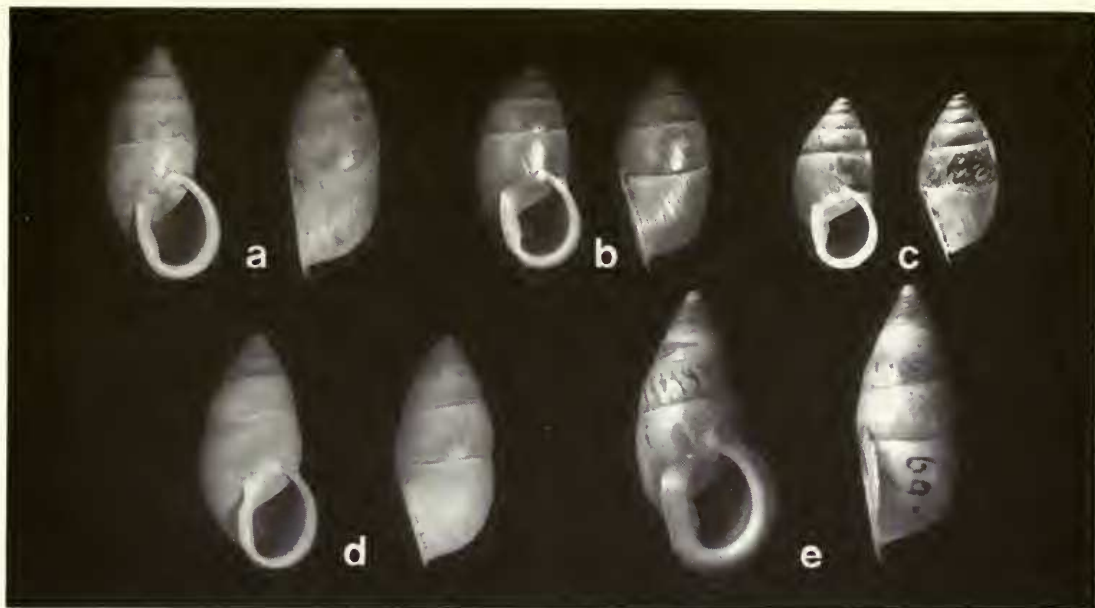
Fig. 25 *Euryptyxis labiosa:* a-c, Tawai Atair, Oman, BMNH; d, Dumsuk Island, Read Sea, BMNH 1928.3.16.29; e, holotype of *Bulimulus hypodon* Pilsbry, ANS 23029. All × 1·5.

recently dead (intact periostracum), and long dead (periostracum lost) collected at Tawai Atair in 1978, (Table 6). Despite small sample size, there were highly significant differences between the long-dead category and each of the other two categories for almost all shell parameters, whilst there were few significant differences between the latter pair. There also appear to be geographical differences, at least for some shell characters. Whereas shells from Aden seem to show a similar degree of shape variation to those from Dhofar, the former are typically more elongate and tend to have a wider lip (*c*. 2 mm. compared with 1–1·5 mm. for Dhofar).

Body. Darkly pigmented, becoming almost black towards head region.

Lung cavity. Similar to other *Euryptyxis* species, with kidney extending 0·75–0·8 times length of lung (Table 3). Outer lung wall strongly pigmented with black and opaque white irregularly shaped patches, clearly visible through shell (Mordan, 1980b: pl.2).

Radula (Figs 26a–b). Overall size of radula markedly smaller than in other *Euryptyxis,* but individual tooth size not greatly different; total number of teeth per row lower because fewer marginals (Table 2).

Reproductive system (Fig. 27). Albumen gland about half length of spermoviduct, and spermatheca only slightly longer than free oviduct. Relative length of vagina/atrium complex as in other *Euryptyxis* but much wider, being more than twice width of free oviduct. Details of terminal male system similar to *E. latireflexa,* although overall dimensions much smaller.

Differences as follows: number of pits in epiphallus greater, being 30–31 (Table 5; Fig. 27c); appendix enters higher up penis; appendicular retractor does not ensheath mid-portion of appendix prior to insertion. Arrangement of pillasters within penis similar to *E. latireflexa,* but a well-defined transverse groove just below epiphallar pore separates pair of lateral pillasters surrounding pore from their downward extensions (Fig. 27B); pilaster pattern within base of appendix as in *E. latireflexa.*

COMMENTS. In both shell and soft anatomy this species most closely resembles *latireflexa,* with which it co-occurs in Dhofar, but at Tawai Atair there are differences in penial and epiphallar anatomy, and the adult shell is distinctly smaller throughout its range.

Table 6 Comparison of shell dimensions in living, recently dead, and long-dead shells of *Euryptyxis labiosa* from Tawai Atair, Dhofar, Oman, 30.iv.1978. Student's t Test (unequal variance).

Parameter	Living (n=3)		Rec. dead (n=8)		Long-dead (n=6)		Living/ long-dead		Living/ rec. dead		Rec. dead/ long-dead	
	x	s.d.	x	s.d.	x	s.d.	t	d.f.	t	d.f.	t	d.f.
Shell ht.	17·03	0·84	16·92	0·84	20·62	5·7	8·11	5 ***	0·23	7 ns	9·81	14 ***
Shell max. diam.	9·23	0·31	9·24	0·26	10·68	5·2	5·26	9 ***	0·2	4 ns	6·25	8 ***
Shell min. diam.	7·6	0·27	7·94	0·31	9·0	5·1	5·39	9 ***	1·8	6 ns	4·5	9 **
Apert. ht.	8·63	0·21	8·62	0·45	9·81	4·5	5·62	9 ***	0·4	11 ns	5·1	13 ***
Apert. diam.	6·47	0·25	6·48	0·24	7·5	2·3	5·92	5 **	0·12	5 ns	7·8	13 ***
Lip width	1·17	0·12	1·15	0·11	1·28	0·18	1·16	9 ns	0·22	5 ns	1·58	8 ns
No. whorls	6·06	0·25	6·38	0·13	6·59	0·39	4·17	6 **	1·92	3 ns	4·75	8 ns
Spire Index	2·24	0·03	2·13	0·13	2·3	0·13	1·01	9 ns	2·25	9 ns	2·39	13 *

***p<0·001
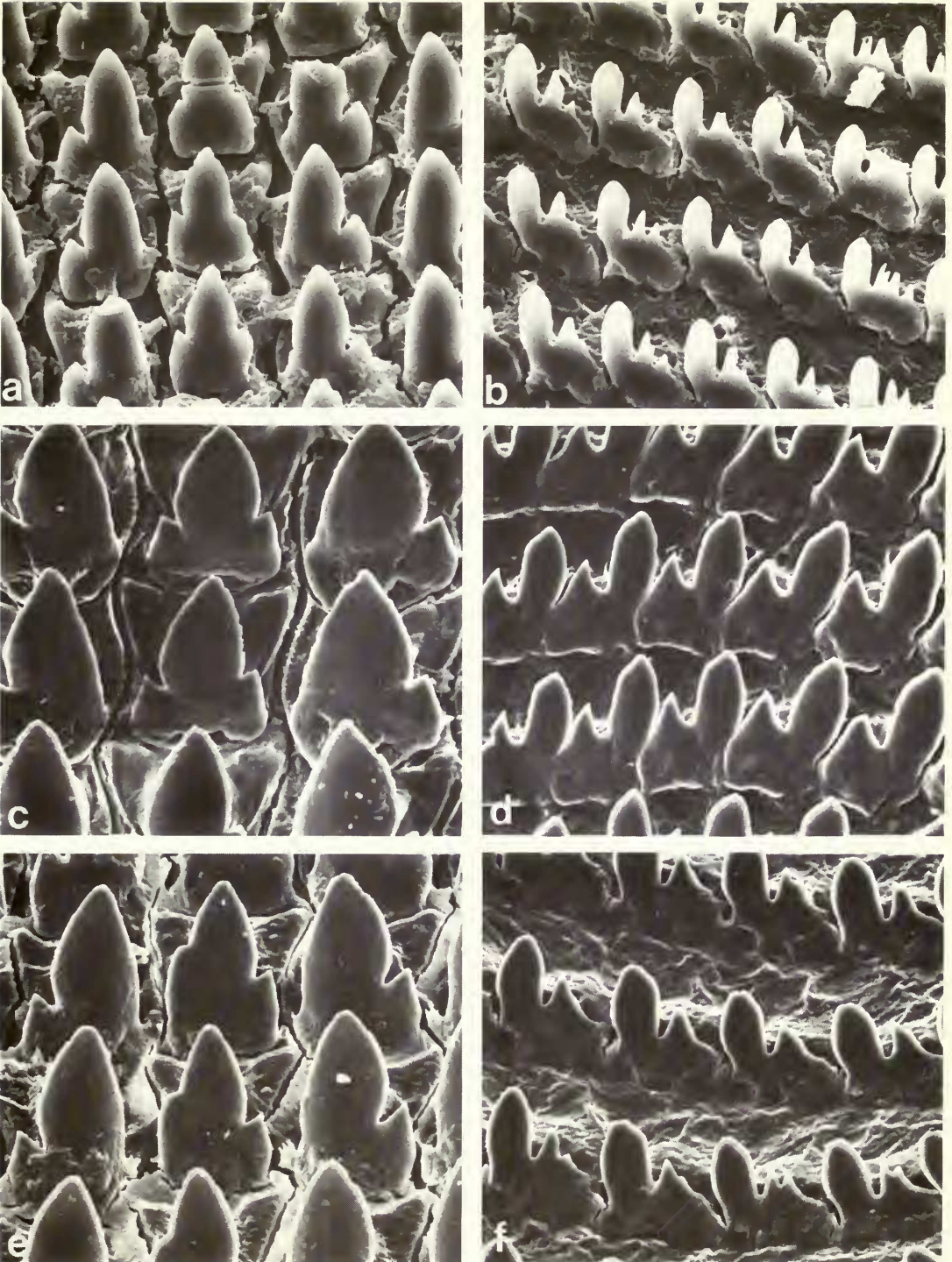**p<0·01
*p<0·05
ns not significant

Fig. 26 Radular teeth of *Euryptyxis:* a, *E. labiosa,* Tawai Atair, Oman, 30.iv.1978, central and lateral teeth; b, marginal teeth; c, *E. latireflexa,* Tawi Atair, Oman, 30.iv.1978, central and lateral teeth; d, marginal teeth. e, *E. latireflexa,* Ain Arzat, 31.v.1976, central and lateral teeth; f, marginal teeth; ×720.
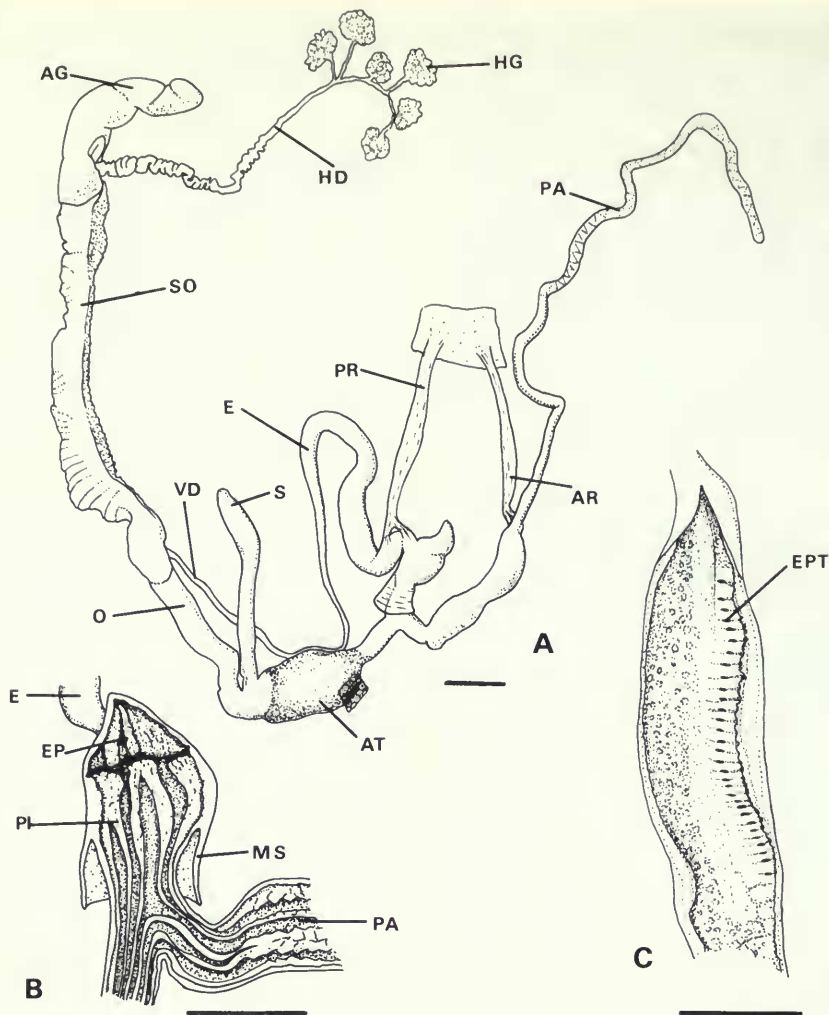
Fig. 27   *Euryptyxis labiosa,* Tawi Atair, Oman, 1978: A, Genital system; B, Penis; C, Epiphallus. Scale
1 mm.

Euryptyxis latireflexa (Reeve, 1849)

Bulimus latireflexus Reeve, 1849, pl. LXXVII, species 568. [Muscat?].
Bulimus latireflexus Reeve. Bourguignat, 1882:19, fig. 22.
Bulimus micraulaxus Bourguignat, 1882:17, fig. 20. [sud de Arabie].
Bulimus micraulaxus Bourguignat. Westerlund, 1887:62.
Buliminus lunti Melvill, 1894:224, pl. XIV, fig. 7. [Plateau 400 miles east of Aden, Hadramaut]. Melvill &
    Ponsonby, 1896:1.
Bulimus (Petraeus) lunti Melvil. Rossmässler, 1896:96, pl. 207, fig. 1305.
Bulimus deflersi Jousseaume, 1894:100. [Gebel el Areys].
Petraeus socialis Jousseaume, 1899:8. [Schoukra].
Petraeus schoukraensis Jousseaume, 1899:8. [Schoukra].
Buliminus (Petraeocerastus) schoukraensis Jousseaume. Kobelt, 1902:989.
Bulimus (Petraeomastus) socialis Jousseaume. Kobelt, 1902:991.
Cerastus dinshawi Sykes, 1902:338. [Senna].
Buliminus (Petraeocerastus) dinshawi Sykes. Rossmässler, 1906:58, pl. 329, fig. 2061.

Euryptyxis lunti var. *makallensis* Pallary, 1925:224, pl. XXXV, fig. 22. [Makalla; Gebel el Da'liya].
Euryptyxis littlei Pallary, 1925:224, pl. XXXV, fig. 21. [Gebel el Da'liya; Gebel Mihta; Qarn el Ghail].
Euryptyxis littlei var. *minor* Pallary, 1925:224. [as above].
Euryptyxis leesi Pallary, 1928:41, pl. 1, figs a,b. [Dhofar].
Euryptyxis dinshawi Sykes. Connolly, 1931:41. Fisher-Piette & Métivier, 1972:1293, pl. 1, figs 10–13.
Euryptyxis deflersi Jousseaume. Fisher-Piette & Métivier, 1972:1292, pl. 1, figs 18–20.
Euryptyxis latireflexus Reeve. [*pars*]. Fisher-Piette & Métivier, 1972:1294, pl. 1, figs 14, 16.
Euryptyxis leesi Pallary. Fisher-Piette & Métivier, 1972:1295, pl. 2, figs 27–36.
Euryptyxis schoukraensis Jousseaume. Fisher-Piette & Métivier, 1972:1300, pl. 2, figs 24–26.
Euryptyxis socialis Jousseaume. Fisher-Piette & Métivier, 1972:1301, pl. 2, figs 21–23.
Euryptyxis candida Lamarck. Mordan, 1980b:106, pl. 1.

TYPE MATERIAL. Lectotype (Here selected, BMNH 1984159) and 2 Paralectotypes (BMNH 1984160) *latireflexus* Reeve, ? Muscat, Oman, Cuming Collection. Two syntypes *lunti* Melvill, Hadramaut, leg. W. Lunt, 1893–4, BMNH 1895.7.10.2–3. Lectotype and 3 Paralectotypes *socialis* Jousseaume, Schoukra, South Yemen, MNHN (selected Fisher-Piette & Métivier, 1972:1302). Lectotype and 2 Paralectotypes *schoukraensis* Jousseaume, Schoukra, South Yemen, MNHN (Selected Fisher-Piette & Métivier, 1972:1300). Holotype *deflersi* Jousseaume, Jebel el Arays, leg. Deflers, MNHN. Holotype *dinshawi* Sykes, Senna, ? South Yemen, leg. E. R. Shopland, BMNH 1903.6.8.7. Six syntypes *leesi* Pallary, Dhofar, Oman, leg. G. M. Lees, BMNH 1928.2.25.1–7.

The type locality of the senior synonym, *latireflexa* Reeve, is uncertain, but clearly that of Muscat given in the *Conchologica Iconica* is erroneous. Specimens closely resembling the types have been recorded from localities as far apart as Qairoon Hairiti, Dhofar (Fig. 28b) and Qubesh, Yemen.

OTHER MATERIAL. **Yemen:** Al Barh, 50 km. W. Taizz, leg. J. Lavranos, 1977, MNHN, (12 specs.), 1978, MNHN, (1 spec.); 45 km. from Taizz, on road to Turba, leg. J. Lavranos, 1978, MNHN, (2 specs.); Marfaq, between Taizz and Hodeida, leg. J. Lavranos, 1978, MNHN, (2 specs.); Qubash, 1700 m, leg. Lavranos, 1979, MNHN (1 spec). **South Yemen:** Hadramaut, leg. W. Lunt, 1893–94, BMNH 1895.7.10.4, (1 spec.), NMW 55.158, (7 specs.); Jebel Jihaf, 7000 ft., leg. H. Scott, ix–x.1937, BMNH, (4 specs.); Jebel Harir, 7500 ft., leg. H. Scott, 4.x.1937, BMNH, (2 specs); Dhala, 1500 m., leg. H. Scott, 12–14.ix.1937, BMNH, (5 specs.) **Oman:** Dhofar, leg. Mrs J. T. Bent, 1894–5, BMNH 1898.12.4.20, (1 spec.); Dahaq Thu'ari, Jabal Qara, leg. C. Bertram, BMNH 1948.5.28.1–5, (5 specs., 2 dissected); Salala, leg. P. Cambridge, 1966, BMNH, (2 specs.); Dhofar, leg. Fuller, iii.1978, ZMC, (3 specs.); Ain Arzat, Jabal Qara, 80 m., leg. P. B. Mordan, 31.v.1976, BMNH 1982, (numerous specs, 10 dissected); Khadrafi, Jabal Qamr, 760 m., leg. P. B. Mordan, 2.vi.1976, BMNH 1982, (numerous specs., 9 in spirit, 3 dissected); Jabal Qara, leg. D. J. Greathead, 3.xi.1976, BMNH, (5 specs.); Wadi Darbat, Jabal Qara, leg. M. D. Gallagher, 20.x.1977, BMNH, (2 specs.); Wadi Sayq, Jabal Qmar, 20 m, leg. M. D. Gallagher, 26.ix.1977, 3.v.1978, BMNH, (5 specs); near Raysut, 100 m, leg. M. D. Gallagher, 6.ix.1977, BMNH, (1 spec.); Wadi Nahiz, Jabal Qara, 500 m, leg. M. D. Gallagher, 27.vi.1977 and R. P. Whitcombe, 21.ix.1979, BMNH, (5 specs.); Tawi Atair, Jabal Samhan, leg. M. D. Gallagher, 9.iv.1977 and 30.iv.1978, BMNH 1982, (numerous specs, 3 in spirit, 2 dissected); WNW Salalah, leg. M. Laferiere, 15.xii.1981, MNHN, (5 specs, 1 dissected); Quiroon Hiriti, Jabal Qara, leg. R. M. Lawton, 9.vi.1982.

DISTRIBUTION (Fig. 17). This species would appear to be the most widely distributed Arabian *Euryptyxis*, extending right across the south of the peninsula from the near the west coast to easternmost Dhofar. It inhabits both coastal and mountainous situations.

DESCRIPTION. Dextral; *globose to elongate conic*; surface with regular radial ribbing, *typically becoming weaker and less regular towards the aperture*, and fine regular spiral striae which cross the ribs; protoconch starting smooth, becoming ribbed; umbilicus closed. Aperture with *well-developed recurved lip*, may be greatly expanded; *strong columellar tooth in body whorl* (Fig. 18A). Colour opaque white to brown, aperture more deeply pigmented.

Shell. Dimensions: Lectotype *latireflexus* Reeve (Fig. 28a): $31.8 \times 15.1 \times 12.5$; 14.9×11.1; lip 2.2; 8.2 wh. Paralectotypes: $28.1 \times 14.0 \times 11.6$; 14.0×10.6; lip 2.3; 7.9 wh.; $28.9 \times 14.0 \times 12.1$; 13.4×10.4; lip 2.2; 8 wh. Syntype *lunti* Melvill (Fig. 28c): $27.6 \times 15.2 \times 12.0$; 14.8×11.5; lip 3.1; 8 wh. Lectotype *socialis* Jousseaume: $34.3 \times 17.3 \times 12.7$; 19.2×14.2; lip 3.5; 8.1 wh. Lectotype *schoukraensis* Jousseaume: $34.8 \times 17.7 \times 13.0$; 18.7×13.7; lip 3.6; 8 wh. Holotype *deflersi* Jousseaume: $30.7 \times 16.8 \times 12.7$; 16.5×12.5;

Fig. 28 a, Lectotype of *Buliminus latireflexus* Reeve, BMNH 1984159; b, *Euryptyxis latireflexa,* Qubesh, Yemen, 1979, NMHN; c, figured syntype of *Buliminus lunti* Melvill, BMNH 1895.7.10.2; d, holotype of *Cerastus dinshawi* Sykes, BMNH 1903.6.8.7; e. *E. latireflexa,* Twai Atair, Oman, 1978; f, syntype of *E. leesi* Pallary, BMNH 1928.2.25.1. All × 1·5.

Table 7 Comparison of shell parameters in living populations of *E. latireflexa* from the three principal mountain ranges in Dhofar.

	1. Tawai Atair Jabal Shamhan 30.iv.1978 (n = 5)		2. Khadrafi Jabal al Qmar 2.vi.1976 (n = 8)		3. Ain Arzat Jabal Qara 31.v.1976 (n = 16)		4. Dahq Thu'ari Jabal Qara 27.1v.1977 (n = 10)		Anovar 1/2/3	Student's t 3/4	
	x	s.d.	x	s.d.	x	s.d.	x	s.d.	F	d.f.	t
Shell ht.	27·82	1·19	22·18	1·49	26·23	0·81	25·76	2·0	40·59 ***	11	0·17 ns
Sh. max. diam.	16·26	0·35	16·58	0·86	16·94	0·67	15·85	1·1	2·14 ns	14	2·83 ns
Sh. min. diam.	13·48	0·30	13·5	0·89	13·69	0·58	13·59	0·9	0·34 ns	14	0·29 ns
Apert. ht.	15·56	0·81	13·4	0·87	16·36	0·64	15·76	1·28	43·26 ***	12	1·37 ns
Apert. diam.	11·68	0·86	10·44	0·74	13·63	0·62	12·59	1·08	64·14 ***	14	2·77 ns
Spire Index	2·06	0·11	1·66	0·05	1·91	0·1	1·89	0·08	35·70 ***	23	0·81 ns

***p < 0·001
ns not significant

lip 2·8; 8 wh. Holotype *dinshawi* Sykes (Fig. 28d): 36·1 × 22·0 × 14·3; 20·7 × 17·5; lip 5·8; 8 wh. Largest Syntype *leesi* Pallary: 27·8 × 17·3 × 13·7; 15·8 × 13·0; lip 3·5; 7·4 wh. Figured syntype (Fig. 28f): 24·7 × 16·0 × 13·5; 15·8 × 13·0; lip 2·7; 7·5 wh.

Shell shape varies considerably within the species, apparently along broad clines. In Dhofar, from where there is a considerable amount of material, statistically significant differences in shell shape were found between roughly contemporary representative samples from the three prinicipal mountain ranges; Jabal Qamar, Jabal Qara and Jabal Samhan (Table 7).

Specimens from Yemen and South Yemen to the west are noticeably more conical than the 'globular' form *leesi* Pallary from Dhofar (Fig. 28f), and often have a very much more developed apertural lip, culminating in the extreme form *dinshawi* Sykes found at Dhala, South Yemen (Fig. 28d).

Body. Pigmentation restricted to tips of tubercles, which are speckled with pale brown; colour darker in head region.

Radula (Figs 26c–f). Table 2 clearly shows distinct differences in tooth size between specimens from Tawai Atair and from Ain Arzat, Dhofar, the former being the larger; it may or may not be significant that at Tawai Atair *E. latireflexa* is sympatric with the smaller *E. labiosa*. Overall radular morphology similar to *E. candida*.

Lung cavity (Figs 29A–B). Kidney of typical orthurethran form, extending from top of lung downwards about 0·75–0·8 times length of cavity (Table 3). Fold of epithelium, up to 1 mm tall, runs from renal pore upwards parallel with kidney almost to top as renal fold, and then reflexes to run downwards alongside rectum as rectal fold. At pneumostome fold turns sharply away from rectum before stopping. Pneumostome fairly complex (Fig. 29B) bearing transverse fold of mantle which emerges from anus. Venation strongly developed, as in other cerastuines. Outer lung wall weakly pigmented with occasional flecks of opaque white.

Reproductive system (Figs 30, 31) Hermaphrodite gland composed of between 5 and 7 irregularly shaped lobes. Albumen gland from 0·5 and 0·8 times length of spermoviduct, and free oviduct about twice length of vagina and two-thirds length of spermatheca. Epiphallus approximately 4 to 5 times length of penis, and only weakly ridged externally; internally with single row of 17 to 28 pits (Fig. 31A; Table 5). Penial caecum conical, varying in height from 0·3 to 0·5 times length of penis; muscular sheath never recurved. Penial and appendicular retractor muscles originate separately on lower lung wall; former divides, two small branches inserting on epiphallus, and main branch on penis proper.
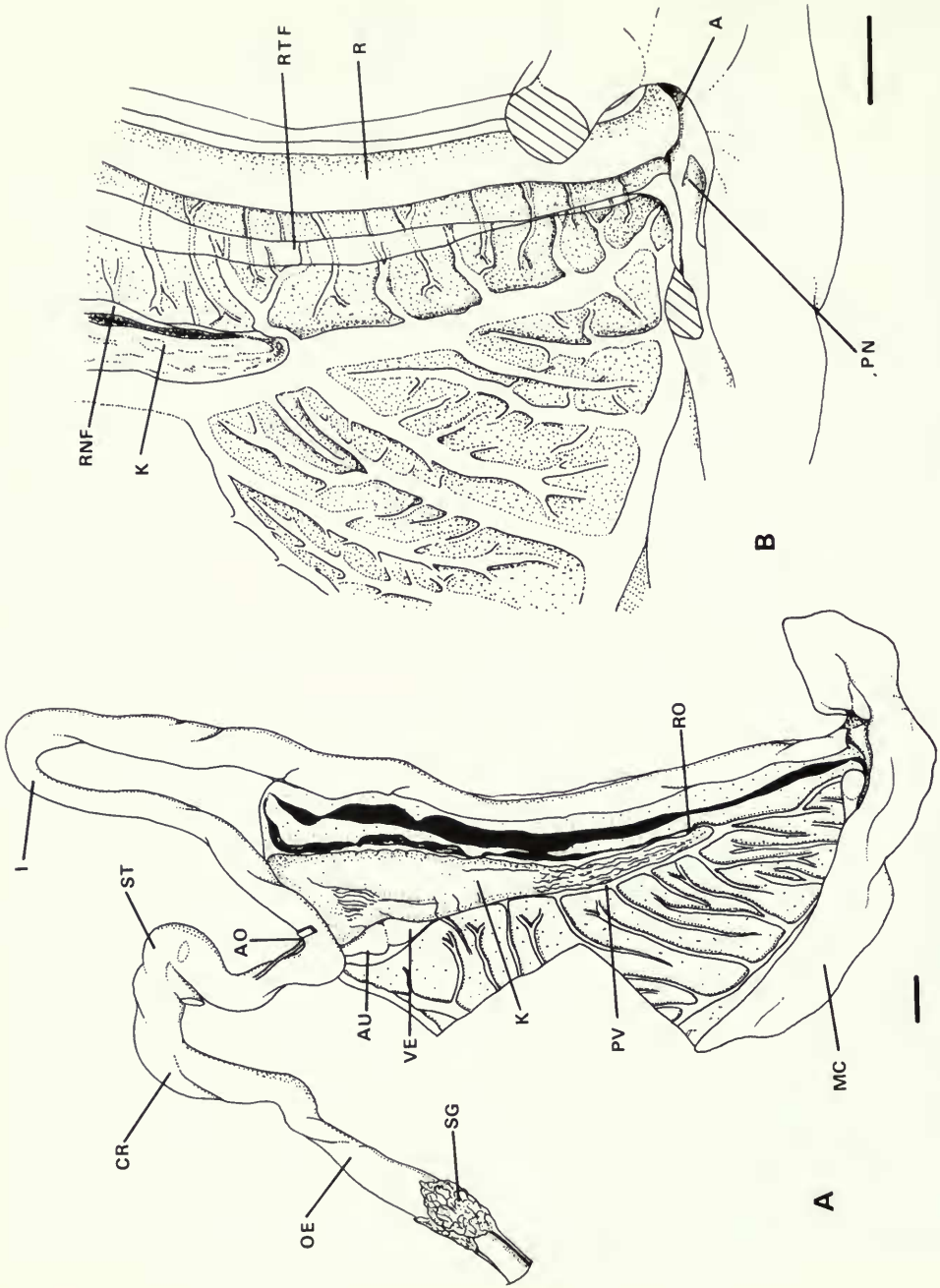
Fig. 29 *Euryptyxis latireflexa*, Ain Arzat, Oman, 1976: A, lung and alimentary system; B, pneumostome region. Scale 2 mm.
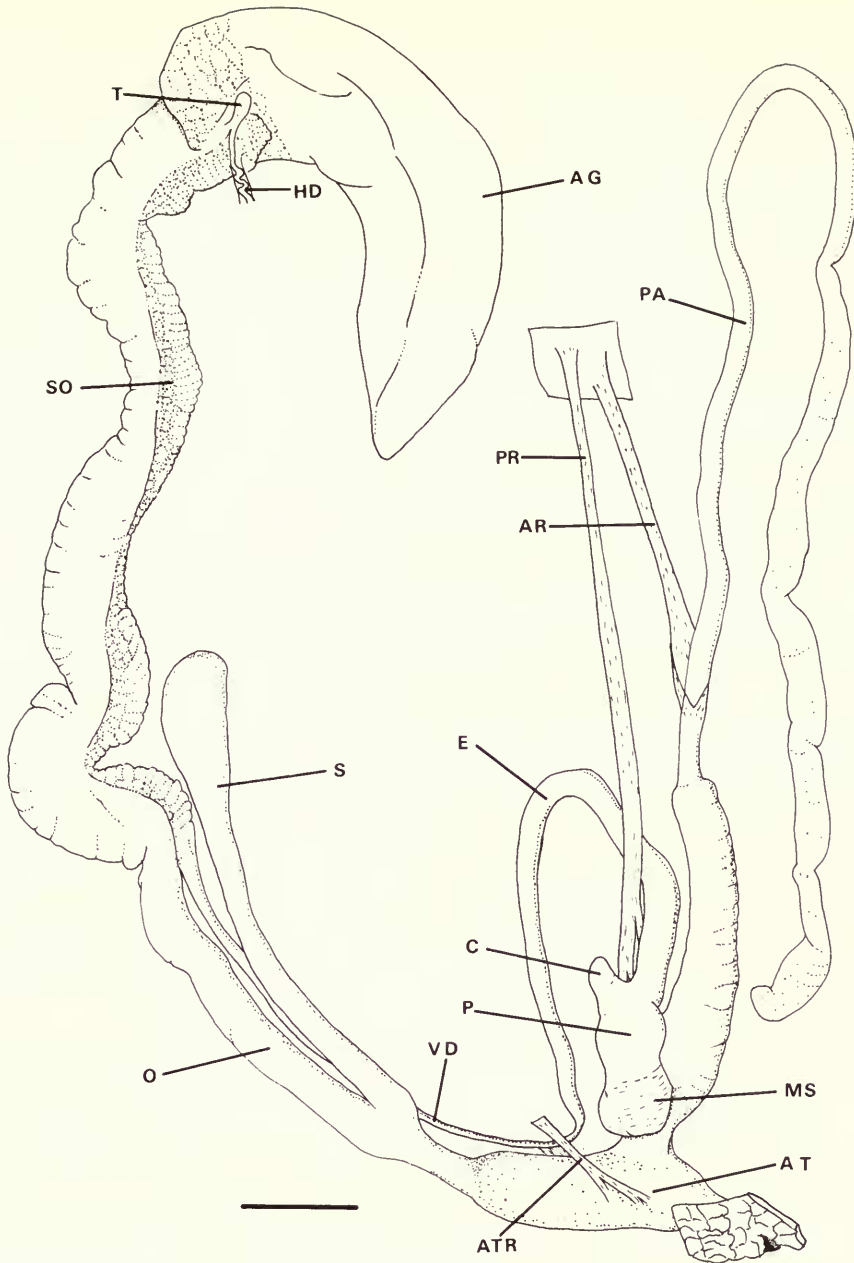
Fig. 30   Genital system of *Euryptyxis latireflexa,* Ain Arzat, Oman, 1976. Scale 2 mm.

Appendix enters penis about one-third the way up and offset from epiphallar pore; its basal region carries 5–6 wavy, longitudinal pillasters, and retractor muscle surrounds lower part of central portion of appendix for a short distance before inserting at its junction with basal region (Fig. 31B). Internal pilaster pattern of penis appears symmetrical (Fig. 31C): on either side of epiphallar pore an elongate glandular area extends upwards almost to top of caecum; just below pore the two fuse for a short distance, only to divide and continue downwards as tapering
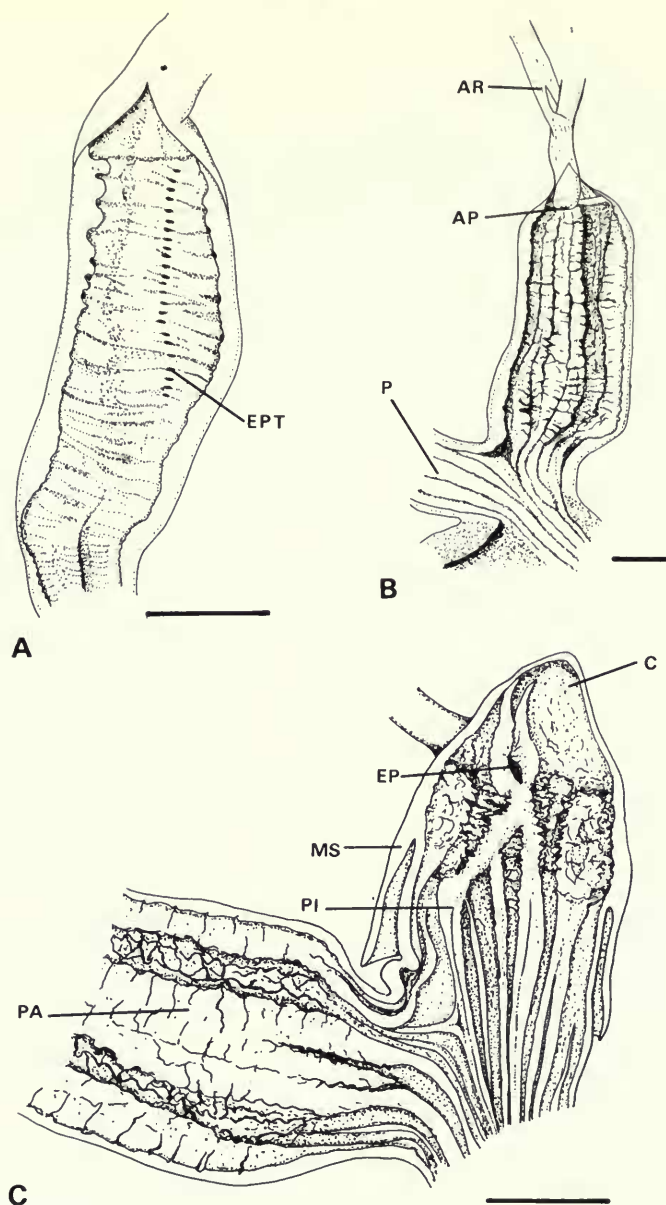
Fig. 31 *Euryptyxis latireflexa*, Ain Arzat, Oman, 1976: A, epiphallus; B, base of penial appendix; C, penis. Scale 1 mm.

pilasters. Also two large glandular patches with associated pilasters, just as in *E. candida,* and one or two intermediate glandular areas.

COMMENTS. *E. latireflexa* as recognised here includes numerous synonyms, and in most cases their present inclusion is based on shell characters alone. Anatomical information is only available from Dhofar, but a detailed study of this suggests that only one species is present there, despite considerable shell variation (Table 7). West of Dhofar there appears to be a clinal increase in shell height and lip width. Although there are a relatively large number of shells recorded from the region of Dhala, the intervening area of South Yemen is poorly known with only the shells

collected by Little around Al Mukalla (figured in Pallary, 1925) and Lunt from the Hadramaut (Melvill, 1894).

This species most closely resembles *E. labiosa*. It is however always larger than *labiosa* and differs from it anatomically in the number of epiphallar pits and the relative proportions of the penis, as well as mantle and body pigmentation.

E. revoili Bourguignat from Somalia has a similar number of epiphallar pits to *latireflexa* (Table 5), as well as showing conchological similiarities, but differs significantly in the reproductive anatomy, notably in the insertion of the penis retractor muscle which is on the epiphallus only.

ACHATINELLOIDES Nevill, 1878

TYPE SPECIES. *Bulimus socotrensis* Pfeiffer [monotypy].

DIAGNOSIS. Shell with undifferentiated lip. Penis with short, rounded caecum; penial retractor inserts on epiphallus; appendicular retractor inserts on basal portion of appendix, and originates separatey from penial retractor.

Achatinelloides sebasmia (Jousseaume, 1889)

Ovella sebasmia Jousseaume, 1889:350. [Aden].
Ovella sebasmia Jousseaume, 1890:94, pl. 3, fig. 9–11.

TYPE MATERIAL. 2 Syntypes, Aden, South Yemen, Jousseaume Collection, MNHN.

DISTRIBUTION. Known only from the type locality (above).

DESCRIPTION. Dextral, elongate-conic; surface with regular, coarse, radial ribs, protoconch smooth; umbilicus open. Aperture elongate-oval, lip undifferentiated, thick callus extending across parietal wall and small parietal denticle developed near palatal/parietal border; weak columellar fold. Colour creamy white with irregular, brown, flammulate patterning, weaker on body whorl; protoconch white, sometimes pale brown on lower part of whorl; aperture pale brown internally.

Shell. Dimensions of figured syntype (Fig. 32a): $17\cdot8 \times 9\cdot2 \times 8\cdot2$; $9\cdot6 \times 4\cdot8$; $7\cdot2$ wh. Second specimen immature.

Anatomy. Unknown.

COMMENTS. See under *jousseaumei* below.

Achatinelloides jousseaumei (Jousseaume, 1890)

Ovella jousseaumei Jousseaume, 1890:93, pl. 3, figs 7, 8. [Mahala].

TYPE MATERAL. Syntypes, Mahala, Bourguignat Coll., MNHN, (1 specimen); Aden, Jousseaume Colln. MNHN, (6 specimens).

DISTRIBUTION. Known only from the type material.

DESCRIPTION. As for *sebasmia* above but more globose, with stronger colour patterning on body whorl, and more-developed columellar fold.

Shell. Dimensions of the two mature syntypes (Fig. 32b): $20\cdot2 \times 11\cdot9 \times 10\cdot1$; $11\cdot3 \times 6\cdot3$; 7 wh. [Bourguignat Colln., possible figure.] $19\cdot4 \times 11\cdot0 \times 10\cdot1$; $11\cdot1 \times 6\cdot3$; 7 wh. [Jousseaume Colln.] Remaining syntypes immature.

Anatomy. Unknown.

COMMENTS. The genus *Achatinelloides* represents an endemic radiation on the islands of Socotra and Abd al Kuri, with a total of seventeen species being recognised by Smith (1903). They occupy a variety of habitats at elevations up to 1500 m. It is tempting to think of the Arabian specimens as merely introduced Socotran forms because of their highly restricted distribution around the major South Yemen port of Aden, and the similarity of their shells. Certainly *sebasima* is close to *A. balfouri* Godwin Austen, 1881 (dimensions of the figured syntype, BMNH 1881.12.14.20:
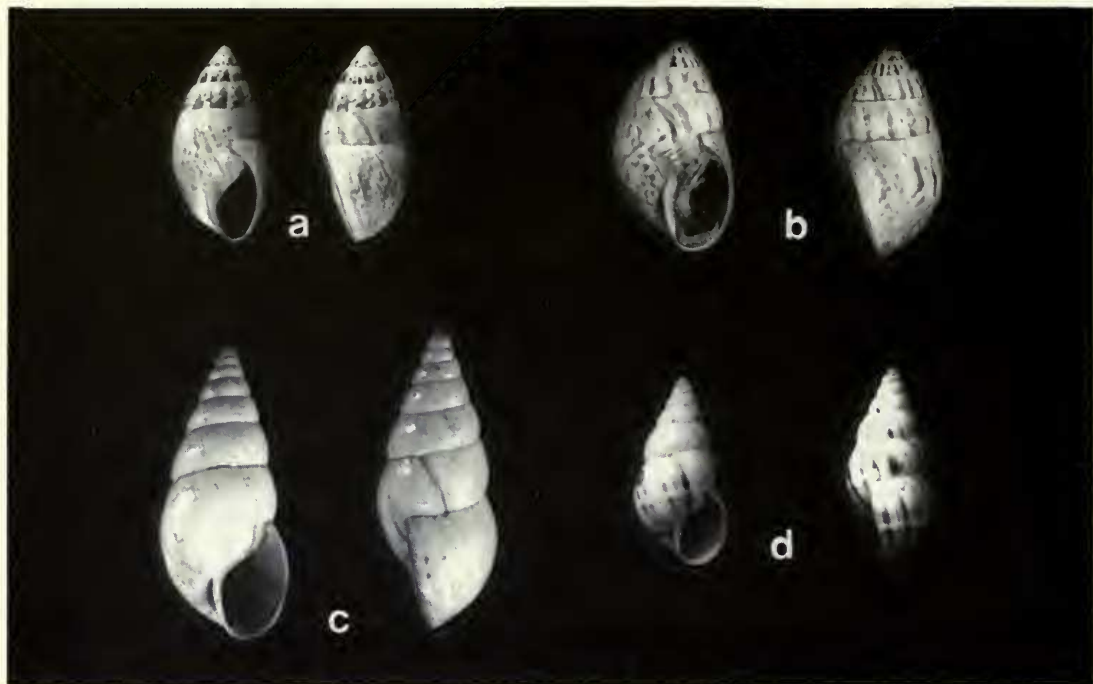
Fig. 32 a, Syntype of *Ovella sebasmia* Jousseaume, MNHN; b, syntype of *Achatinelloides jousseaumei* Bourguignat, MNHN; c, lectotype of *Helix albata* Ferussac, MNHN; d, figured syntype of *Zebrinops ventricosa* Connolly, BMNH 1939.4.19.66. All × 1·5.

20·9 × 10·5 × 10·0; 11·2 × 6·2; 6·7 wh.), and *jousseaumei* is near to both *A. dahamisensis* Smith, 1898 (figured syntype, BMNH 1899.12.20.20: 20·2 × 12·6 × 10·6; 12·4 × 7·3; 6·9 wh.) and *A. homhilensis* Smith, 1898 (figured syntype, BMNH 1899.12.20.51: 19·5 × 11·4 × 10·3; 11·5 × 7·5; 7 wh.).

As the anatomy of *Achatinelloides* has never been investigated, the opportunity has been taken to dissect a poorly preserved aestivating specimen of the type species of the genus, *A. socotrensis* Pfeiffer, 1881, collected on 11.viii.1956 near Hadibu, Socotra (BMNH 1957.7.10.1). The pallial and reproductive anatomy are of the typical cerastine type. The penial and appendicular retractor muscles are separate, but the latter inserts well below the top of the basal portion of the appendix. The penis itself differs from other cerastuines in having three pairs of well-defined longitudinal pilasters in the penial caecum. The caecum is exceptionally thin-walled, the pilaster pattern being clearly visible externally. The penial retractor inserts about one-quarter the way up the epiphallus, which is similar in form to that of *Zebrinops,* and has a single row of approximately 19 internal pits.

ZEBRINOPS Thiele, 1931

TYPE SPECIES. *Limicolaria revoili* Bourguignat [orig. desig.]

DIAGNOSIS. Shell without differentiated lip. Penis with well-developed, elongate caecum; penial retractor inserts on epiphallus. Appendix with long papilla; appendicular retractor inserts on enclosed base of central stalk. Penial and appendicular retractors originate separately.

Zebrinops albata (Férussac, 1827)

Helix (Cochlogena) albata Férussac, 1827:305. [L'Arabie heureuse].
Bulimus albatus Pfeiffer, 1842:42. [Yemen].

Bulimus bicinctus Récluz, 1843a:4. [Socotra].
Bulimus albatus Férussac. Küster & Pfeiffer, 1845–55: 225, pl. 62, figs 7, 8.
Bulimus albatus Pfeiffer. Reeve, 1848:pl. ILI, species 333.
Bulimus candidissimus Pfeiffer, 1858:239. [Socotra].
Zebrinops albatus Connolly, 1941:29.
Zebrinops ventricosa Connolly, 1941:29, pl. 3, fig. 15, text fig. 8. [Dhala].
Zebrinops ventricosa Connolly. Fisher-Piette & Métivier, 1972:1302.
Zebrinops albata Pfeiffer. Verdcourt, 1974:5.

TYPE MATERIAL. Lectotype (here selected) and 2 Paralectotypes *albata* Férussac, 'Arabie Hereuse', leg. Rang, MNHN. Syntypes *ventricosa* Connolly, Dhala, South Yemen, 1500 m, leg. H. Scott, BMNH 1939.4.19.66–79, (13 specs).

OTHER MATERIAL. **Yemen:** El Kubar, leg. G. W. Berry, BMNH 1908.2.21.4–9, (6 specs); Nr Ibb, leg. Haythornthwaite, BMNH 1935.4.4.32–33 (2 specs); 2 km N of Taizz, c 1400 m, leg. H. Scott, BMNH 1939.4.19.80–92, (13 specs, 5 dissected); 17 km E of Taizz, 1100 m, leg. H. Scott, 10.x.1937, BMNH, (10 specs); north of Taizz aerodrome, leg. Brunt & Mather, BMNH, (41 specs); Taizz, leg. P. Heath, 1978, BMNH, (5 specs, 3 dissected); Nr. Hammam Ali, leg. Lavranos, MNHN, (1 spec.). **South Yemen:** Hills near Aden, leg. M. J. Ogle, 1.vii.1903, Godwin–Austen Colln, BMNH, (27 specs); Dhala, leg. Meinertzhagen, xi.1948, BMNH 1954.4.5.1–5, (5 specs).

DISTRIBUTION (Fig. 33). Almost all the material examined originates from two principal areas: the environs of Taizz in North Yemen and Dhala in South Yemen. This may well represent collecting bias, but interestingly the former represents typical *albata* whilst the latter material is largely referable to *ventricosa*. Additional material from near Aden and from Al Kubar, to the south and east of Dhala respectively, is of the *ventricosa* type.

DESCRIPTION. Dextral; elongate conic; umbilicus narrow and shallow. Protoconch smooth; subsequent ornamentation consists only of weak growth lines and occasional malleations; texture glossy. Colour of protoconch often light to dark brown, may be white, remainder opaque white with two interrupted spiral bands of brown (the lower only visible on body whorl) which may extend radially as streaks.

Shell. Dimensions of lectotype (*albata* Férussac) (Fig. 32c): 26·3 × 11·4 × 10·6; 10·1 × 6·6; 8·9 wh. Paralecto-types: 24·6 × 11·3 × 10·0; 10·3 × 6·2 × 8 wh.;   22·5 × 11·3 × 10·6; 9·5 × 5·5; 8·4 wh.   Dimensions of figured syntype (*ventricosa* Connolly) (Fig. 32d): 16·6 × 8·3 × 7·5; 6·7 × 4·6; 7·5 wh.   Dimensions of largest complete specimen, Taizz, leg. Brunt and Mather: 35·2 × 16·5 × 15·7; 15·0 × 9·5; 9·6 wh.

The specific distinction of *ventricosa* was justified by Connolly largely on conchological grounds, principally shell size and shape, but this does not seem to hold up to analysis. The sample collected by Hugh Scott from 2 km north of Taizz comprises mainly good *albata*, but also includes a few smaller specimens. Height against whorl number of this material is plotted in fig. 34, and it can be seen that the two show a clear linear relationship. Additionally, the type specimens of *albata* and *ventricosa* are included in the plot and tend to confirm that the two nominal taxa merely represent age classes of the same species. A statistical comparison of the type series of *albata* and *ventricosa* in respect of the H/D ratio of the shells failed to demonstrate that the latter were significantly more ventricose (Student's t test: 18 degrees of freedom, $t = 0.973$, not significant).

Body. Generally pale, becoming darker towards head region.

Radula (Fig. 35). Both radulae examined extremely worn in central and lateral areas, but marginal teeth in good condition. In all except first two or three marginals of row, ectocones multicuspid. Tooth dimensions and numbers given in Table 2.

Lung cavity. Of typical cerastuine type with well-developed complete renal and rectal folds and prominent venation. Kidney 0·85 times the length of lung. Outer wall clear and unpigmented in most individual, but some have distinct pigmentation in pneumostome region and along rectum.

Reproductive system (Figs 36, 37). Hermaphrodite gland composed of 5 to 6 lobes, and talon sharply curved (fig. 36A). Albumen gland large, approximately 0·9 times length of spermoviduct; latter wider, relative to its length, than in *Euryptyxis*, as is spermatheca which has distinctly
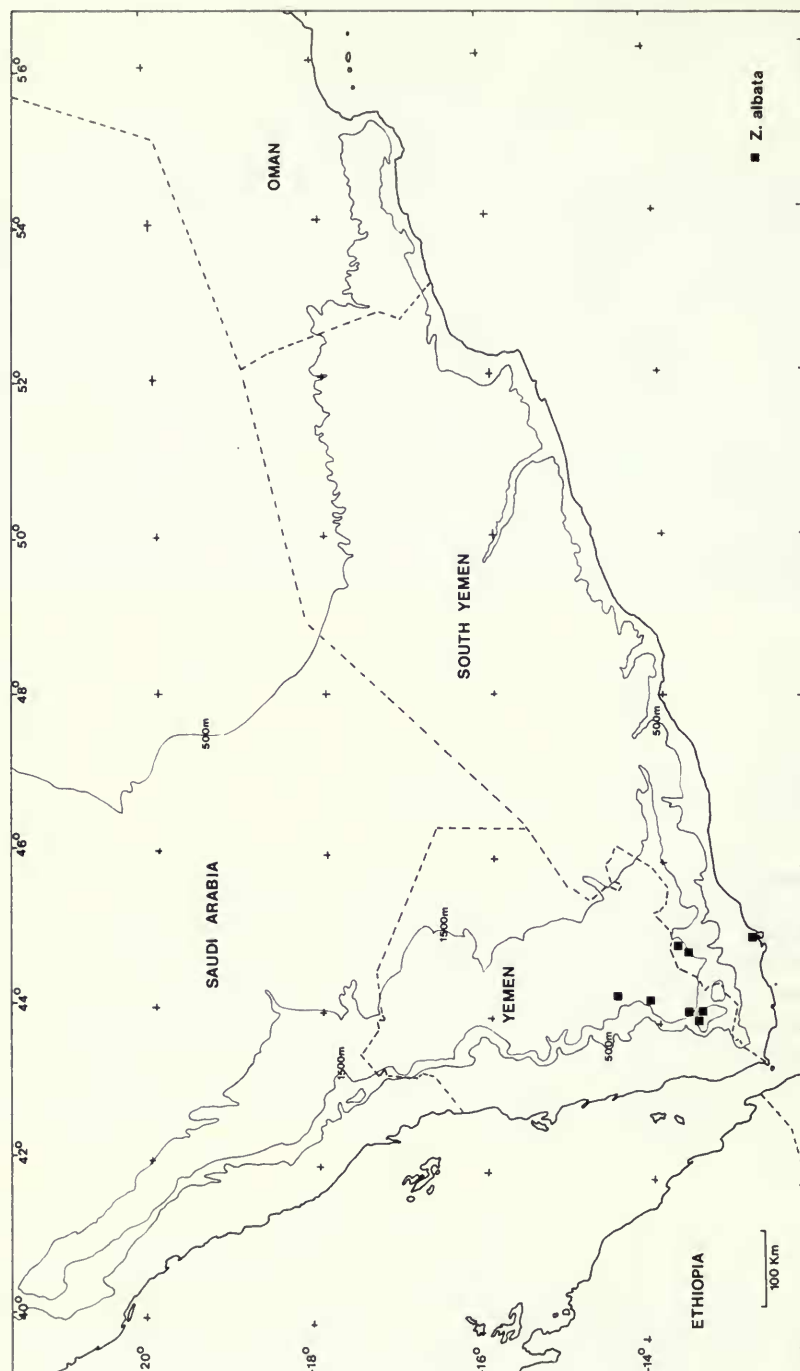
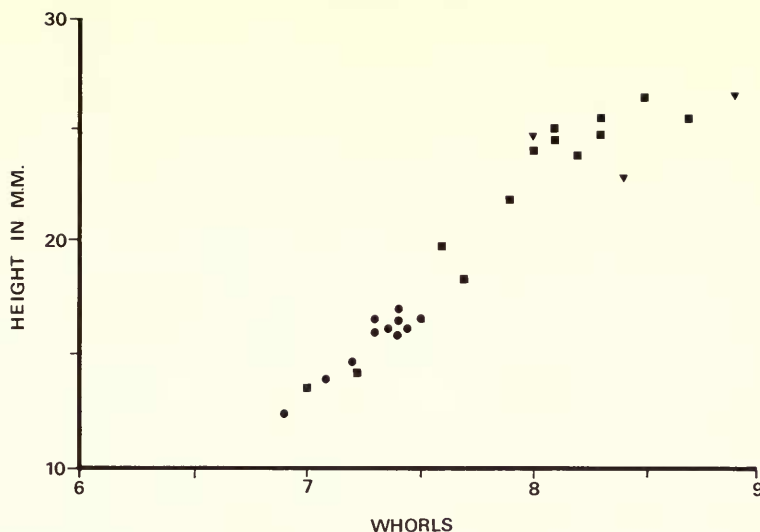**Fig. 33** Distribution map of *Zebrinops albata*.

Fig. 34 Plot of shell height (in mm.) against whorl number for three samples of *Zebrinops albata*. Triangles: type series *Helix albata* Ferussac, Arabia; circles: type series *Zebrinops ventricosa* Connolly, Dhala, S. Yemen; squares: 2 km N. Taizz, Yemen, leg. H. Scott, 10.x.1937, BMNH.
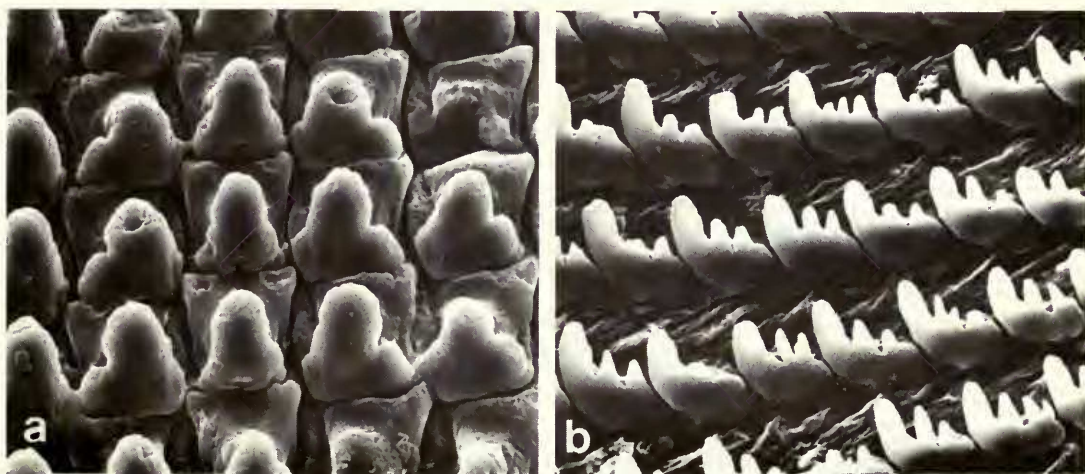
Fig. 35 Radula of *Zebrinops albata*, Taizz, 1978: a, central and lateral teeth; b, marginal teeth; magnification × 720.

globular head. Short spermathecal stalk bears between six and eight strong longitudinal pilasters internally.

Epiphallus massively expanded compared to vas deferens, and bearing longitudinal row of 20–22 strong transverse ridges, the strongest of which are closest to penis and of 'dumbell' shape. These correspond to equivalent number of internal pits (Figs 37B,C), and to spines on spermatophore (Fig. 9A). Penis retractor unbranched and inserts on epiphallus well above penis junction. Externally, penis characterised by large, thick-walled caecum which is as long as penis itself. Internal structure of penis relatively simple (Fig. 37D). Transverse groove at level of

Fig. 36 *Zebrinops albata,* Taizz, Yemen, 1978: A, talon region; B, genital system. Scale 1 mm.

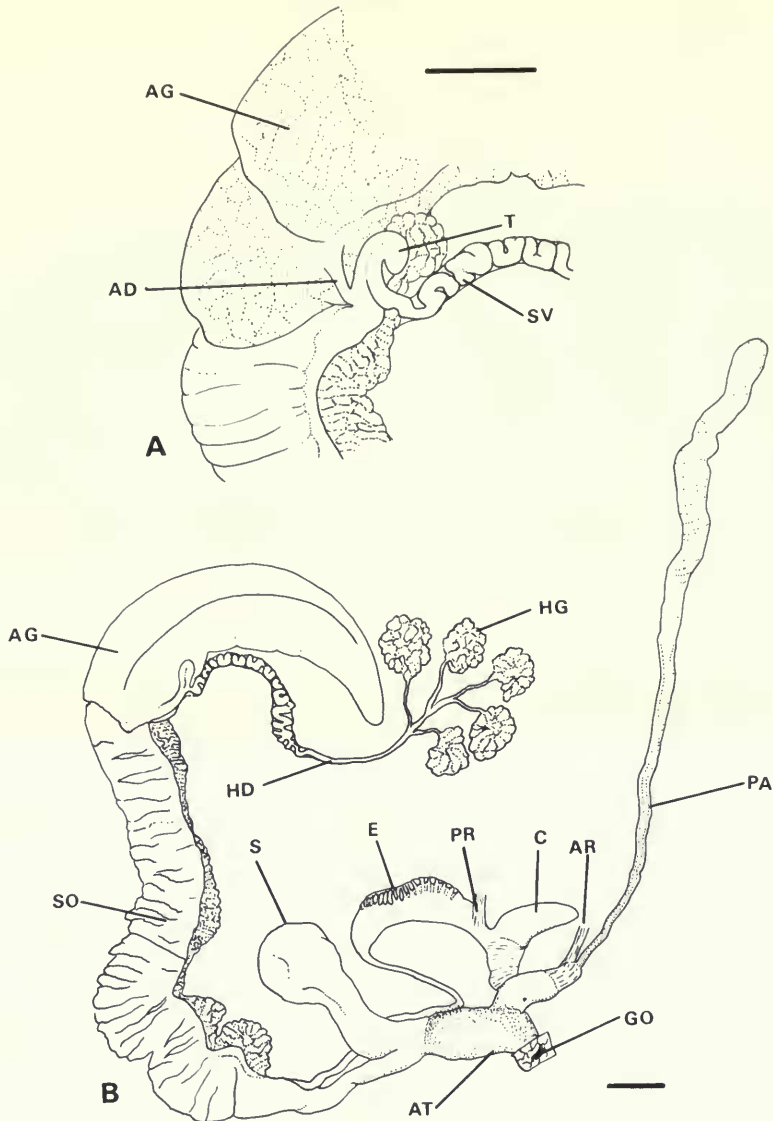epiphallar pore separates caecal area (which bears numerous small, oval glandular patches) from main body of penis which bears 9–10 equal longitudinal pilasters. Penial sheath single-layered.

Appendix inserts broadly on penis below epiphaller pore; short basal portion with regular longitudinal pilasters, and basal part of middle region enclosed by hollow muscular sheath formed from retractor muscle; central stalk projects downwards through septum into lumen of base as long, fine papilla (Fig. 37D).

COMMENTS. There does not appear to be any conchological or anatomical justification for the separation of *albata* and *ventricosa* and therefore the two names are synonymised. The smallest specimen dissected was sexually mature and had a shell height of only 14·2 mm and 7·0 whorls, suggesting that in this group growth is probably not determinate. A number of continental African *Zebrinops* have been dissected and all clearly belong to species other than *albata*.
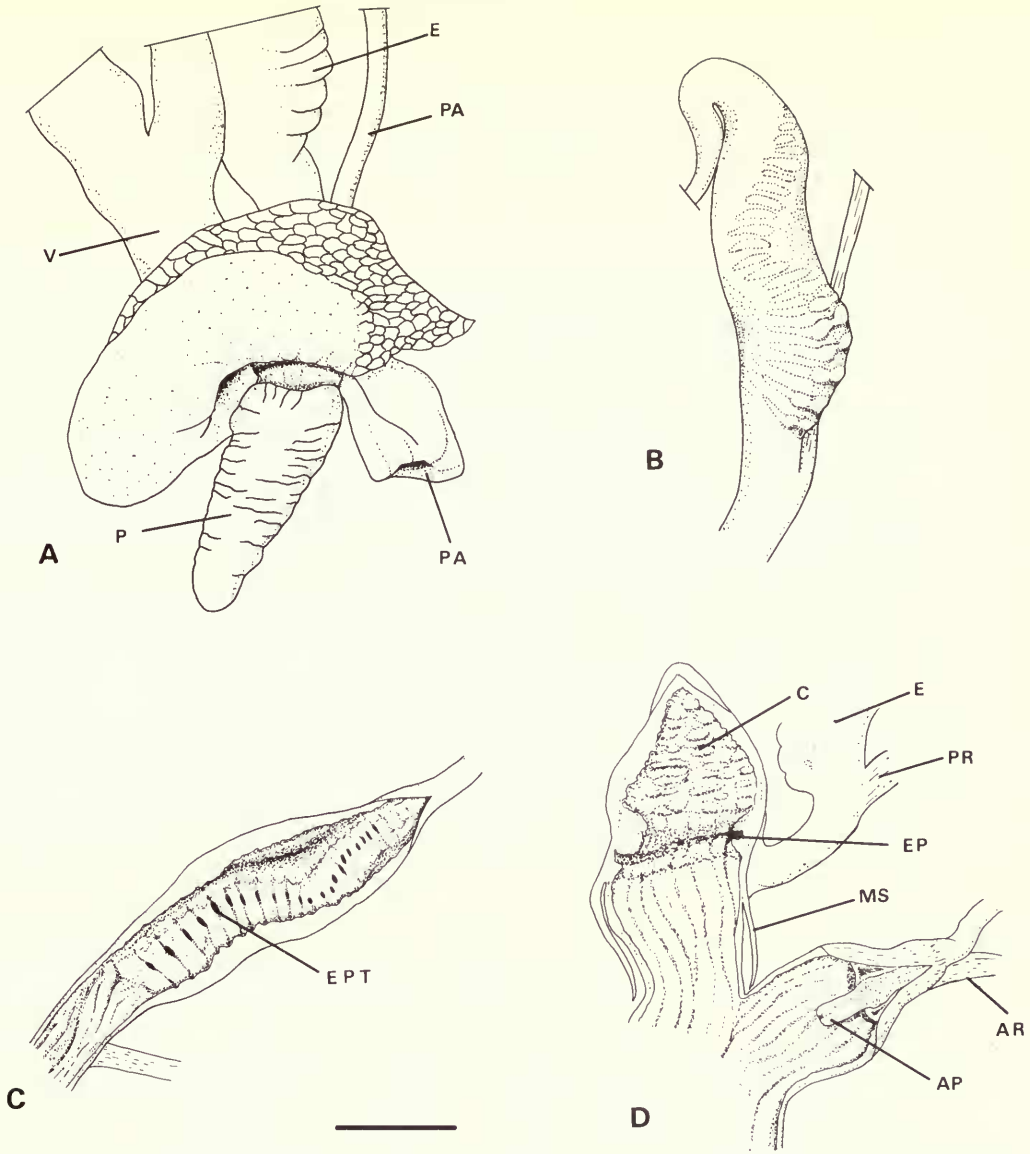
Fig. 37 *Zebrinops albata* Taizz, Yemen, 1978: A, everted genitalia; B, epiphallus, external; C, epiphallus, internal; D, penis and base of appendix. Scale 1 mm.

Discussion

The following discussion addresses two, essentially distinct problems involving decisions made at different taxonomic levels: the problems of species discrimination in arid-habitat land snails; and secondly a consideration of the differences which have been shown to exist between the two major family-group taxa, the Enidae *sensu stricto* and the Cerastinae.

Discrimination at the species level

Shell characters, and more recently characters of the terminal genitalia, have been used to discriminate species of land snails. The former are clearly subject to the effects of environmental

variation, but the relationship between the latter and possible species-isolating mechanisms would appear to be a direct one. Certainly the genitalia have been found pragmatically to be useful in providing low-level taxonomic characters in pulmonates, as well as other animal groups (Arnold, 1973). However, Mayr (1963:103) discounts the importance of mechanical isolation in most cases, suggesting that the observed differences in genital structure are the result of pleiotropy. A possible mechanism by which such pleiotropic changes could be stored by the genitalia, rather than be eliminated by normalizing selection as in other organ systems, has been explored by Arnold (1973, 1983).

Clearly information on soft anatomy is desirable wherever possible, but despite examination of almost all the Arabian pulmonate material currently available in museums, most or all Arabian species in the genera *Cerastus, Achatinelloides, Paramastus* and *Polychordia* are known only from shells, and even for species whose internal anatomy is known, our principal information regarding their geographical distribution and variation is derived from shell collections. Nevertheless, morphological groupings based on shell characters have emerged which are consistent with the limited anatomical information available, and consequently must be regarded as species. The level of confidence in the taxonomy presented here varies greatly between taxa: in the case of the northern Oman enids it is high, for living material was available from a relatively large number of sites throughout the known geographical range, but is much lower in groups such as *Euryptyxis* which are conchologically highly variable and for which anatomical information is available from only a limited part of their assumed distribution.

The high levels of shell variation, so characteristic of many desert groups, stem primarily from two factors: the extreme climatic variability, both spatial and temporal, characteristic of desert environments, and the genetic isolation resulting from the wide separation of most of the populations, often combined with small population size. Reduced gene flow between populations will be accentuated in the larger pulmonate snails considered here, where vagility is reduced further by their habit of aestivating for most of the year attached to rocks or trees, and the analogy has been drawn between the genetics of such semi-sessile animals and that of plants (Selander & Hudson, 1976). Moreover, in periods of extensive mortality these various factors may combine to produce a temporal form of genetic drift, the 'bottle-neck' effect (Cain, 1983), which can cause local fixation of the genotype into a new mode.

Family-level groups

The elucidation of higher-level taxonomy typically requires different, or at least additional characters to those used at the species level, and in this study the pallial cavity and proximal genital system (proximal to the gonad) have been found to be of particular value. Two family-level groups are here defined for the purposes of the discussion: the Enidae *sensu stricto* (comprising the nothern families Eninae and Chondrulinae, *sensu* (Forcart, 1940); and the Cerastinae (or Pachnodinae) *sensu* Zilch, 1959). Any subsequent unqualified use of the term Enidae refers to the former group alone. Consideration of the relationships within the Cerastinae will be deffered until an anatomical study of all the component genera has been completed, and a phylogenetic analysis can be undertaken (Mordan, in prep.).

In the remainder of this discussion, the characters studied are considered system-by-system, rather than in terms of their value at the various taxonomic levels.

Shell

Limited information on shell variation is available for some living populations from Dhofar and northern Oman, where the greatest collecting effort was directed. However, no detailed statistical analysis of shell form and its possible correlation with environmental variables has been attempted, partly because of the lack of an adequate range of sufficiently large samples. Also, no climatic or vegetational data are available for the relevant areas (see Taha *et al.*, 1981, for a summary of Arabian climate). Assemblages of dead shells are generally unsuitable because of uncertainty of their provenance owing to the possibility of passive transport, and even living

populations, at least of some species, appear to comprise adults from a number of year classes which may themselves vary (see below).

Woodruff (1978) has summarised knowledge of variation in the shells of *Cerion,* a West Indian genus with a ecology in many respects similar to the Arabian species, and many of the points he made are relevant to the present discussion. Woodruff considered the shell under the following headings, which for convenience are used here:

Shell size and shape
Populations of all species appear to vary considerably in size of both the adult shell and the aperture, and this is known to be correlated with climate in some other land snail groups (Heller, 1975; Woodruff, 1978; Tillier, 1981). Subtleties of shape are more difficult to quantify accurately, and here the simple height/diameter ratio (the spire index of Cain, 1977) is used; in the subsequent discussion 'shape' refers to this parameter.

Spatial variation in both size and shape is demonstrated in *E. latireflexa* from Dhofar, where roughly contemporary (1976–78) living samples are available from each of the three principal mountain ranges: Jabal Qamar, Jabal Qara, and Jabal Samhan. Analysis of variance shows highly significant inter-population variation in shell height and aperture size between the three mountains, whereas comparison of two living samples from separate sites within the Jabal Qara range shows no such differences (Table 7). Concomitant changes in shape are also recorded between the three mountains, with significantly more globose forms (*leesi* Pallary, Fig. 28f) in Jabal Qamar; as with size, there is no significant difference between populations within the Jabal Qara range (Table 7). This variation may be viewed in a number of ways: as vicariant, in the sense that topography has divided the species into a number of allopatric units which are starting to diverge morphologically, or as points on a cline of increasing shell size running west to east in Dhofar. If the latter is true then the cline reverses for, on the evidence of dead shells, both height and spire index increase westwards from Jebel Qamar, culminating in the form known as *dinshawi* Sykes (Fig. 28d). Alternatively, the observed inter-population differences could be purely random.

Populations of *E. candida* on the Red Sea island of Dumsuk, in the Farsan group, and from the coastal Tihama of Saudi Arabia and Yemen are noticeably smaller than the more typical populations at higher elevations where rainfall is greater, approaching the size of *E. labiosa* (a small, essentially coastal species, which also occurs on Dumsuk). Shell size and shape are also compared in living populations of *Mastus omanensis* and *Imparietula jousseaumei* in N. Oman; in the former no highly significant differences were found (Table 1), but in *I. jousseaumei* significant results have been obtained for all parameters, particularly for shell diameter and spire index (Table 4). Unusually elongate forms of *jousseaumei* were collected from a remote gorge on Jabal Sira (part of Jabal Akhdar, N. Oman) at an elevation of 2400 m. This may simply be part of the general trend for increasing spire index with elevation in this species, but *Pupilla c.f. annandalei* Pilsbry also occurs at this site (the species is otherwise known only from the type locality in Nepal) suggesting perhaps a long-isolated relict fauna in the area (Mordan, 1980b).

Temporal variation in size, but not shape, is also evident in some populations. Significant differences are found for all size parameters (excepting lip width) in comparisons of living and very recently dead shells with shells which had been dead at least one dry season, from a single sample of *Euryptyxis labiosa* from Jabal Samhan, Dhofar. No significant differences exist between the living and freshly dead samples (Table 6). Climate, and in particular precipitation, varies considerably from year to year so that size variation between age classes is not at all unexpected; feeding activity, and thus shell growth, is known to be highly correlated with soil moisture levels in desert snails (Shackak, Orr & Steinberger, 1975).

Shell shape formed the basis of Connolly's separation of *Zebrinops ventricosa* from *Z. albata* (Connolly, 1941), but a statistical comparison of spire indices of the two type series failed to separate them. Similarly, a plot of shell height/maximum shell diameter for the types and a relatively large sample from Dhala, S. Yemen suggests that all form part of a continuous growth series (Fig. 34).

Certain aspects of shape which the spire index fails to distinguish may be useful in separating closely related species: in particular *Euryptyxis fragosa* and *E. candida,* which commonly co-occur in SW. Arabia, differ in the curvature of the sides of the spire profile, the former being more or less flat from the apex down to the body whorl giving a conical profile (Figs 16e–g), the latter markedly convex between the nepionic and body whorls (Figs 16a–d). *Eyryptyxis candida* in particular shows clear ontogenetic shape changes similar to those described by Cain (1981) for certain *Cerion* species, but knowledge of *Euryptyxis* ecology is insufficient to make any suggestions regarding possible adaptive values.

Lip size and shape

Lip expansion is known to be inversely correlated with moisture in some desert snails (Heller, 1975; Woodruff, 1978), and varies greatly between Arabian cerastine species. Although there is no thickening of the lip region in any species, other than the general thickening of the shell which occurs with age in many pulmonate groups (Pollard, 1975), the degree of lip flare or curvature proved a valuable diagnostic character at both generic and specific levels. No lip differentiation is found in either *Zebrinops* and *Achatinelloides,* and is only weakly developed or absent in *Cerastus.* The absence of a differentiated lip makes it impossible to establish maturity from the shell alone, but does not necessarily imply that growth is indeterminate.

Mature *Euryptyxis* always develop a lip, although this ranges from a simple flairing of the aperture in *E. candida* and *E. fragosa* (Figs 16a–g) to a truly recurved structure in *E. labiosa* and *E. latireflexa* (Figs 25, 28). In this last species, the lip can become greatly expanded in some western populations (described under the name *dinshawi* Sykes). The apertural region appears to thicken progressively in most adult snails, and under suitable conditions this could give rise to such extreme lip development. In *Euryptyxis* overall thickening of the shell with age in certain geographical regions also appears to correlate positively with the degree of development of the columellar fold, although there do appear to be overriding intrinsic differences in the size of the fold between individual species (Fig. 18). Both enid species develop lips as adults, but *Mastus omanensis* shows a greater degree of variation in this respect, with one specimen from Qasaydot, Jebel Harim, N. Oman, having an exceptionally expanded lip reminiscent of the *dinshawi* form of *Euryptyxis latireflexa.*

Shell sculpture

This again proved a valuable character in determining species of *Cerastus* and *Euryptyxis.* Of particular value was the relative development and regularity of radial ribbing, and in the case of the latter genus, the extent of development of spiral striae. Three of the species of *Euryptyxis* showed the development of very coarse ribbing in some populations which has given rise to a number of new names from Bourguignat and Jousseaume, but on the evidence of dissections of both smooth and ribbed forms of *E. fragosa* from Taizz, Yemen, such variation comes within the limits of the species as recognised here.

Apical shell sculpture of all species was examined under the stereoscan microscope but showed no taxonomically valuable characters.

Visceral mass

There is considerable variation in the absolute and relative proportions of the shell and visceral mass between genera, expressed in terms of whorl number. Table 3 shows typical lengths of the three principal regions of the visceral mass: the mantle to the top of the lung; the top of the lung to the top of the stomach; and the region above the stomach, which is composed of the posterior lobe of the digestive gland and contains the gonad.

In all genera it is clear that the total visceral mass does not extend to the apex of the shell, and in many species the apical shell whorls are sealed off internally by a septum. In the more-elongate genera *Imparietula* and *Zebrinops* the visceral mass extends relatively further towards the apex than in the shorter forms where the differential between shell and total visceral mass may exceed three whorls. The observed differences between species with elongate and short shells appears to be accounted for by the greater length of the region above the stomach in the former although

additionally the lung of *Imparietula* extends almost two whorls, compared with about one whorl for the other taxa. On the evidence from the species examined, variation does not seem to correlate with family-level groupings.

Alimentary system

Radula

In all species for which there was anatomical material available the radula was examined but little useful information emerged. It is significant that in recent taxonomic revisions of genera in both the Enidae (eg. Heller, 1974; 1975) and Cerastinae (eg. Verdcourt, 1966, 1970; van Mol & Coppois, 1980) the radula has not been used as a diagnostic character at either specific or generic levels. The results are summarized in Table 2.

In *Euryptyxis* both tooth size and number were generally fairly uniform between the three larger species, but in the smallest, *E. labiosa*, where overall radula size was smaller, tooth number, but not size, was distinctly reduced. In *Cerastus* the number of teeth was much as in *Euryptyxis*, but the teeth were generally smaller and the difference in size between the centrals and laterals more pronounced. In *Zebrinops* and *Cerastus* tooth number appeared to vary with size. The radula formula of both enid species was similar, but interestingly the size of individual teeth in *Mastus omanensis*, the larger species, was approximately twice that of *Imparietula jousseaumei*.

At higher taxonomic levels there appear to be no consistent differences between the radulae of many orthurethran groups, although some authors, for example Solem (1962), have referred to a characteristic 'enid' radula. Watson (1920) pointed out the close similarities between the enid radula and that of other Pupillacea, and referred to a generalised radular type characteristic of 'the less-specialised members of the Orthurethra'. This has rows possessing a symetrically tricuspid central tooth with a large, usually pointed, mesocone and markedly smaller outer cusps, and bicuspid laterals with a reduced ectocone, which are typically larger than the central tooth. The marginal mesocone is often very blunt and the ectocone typically with a single cusp which becomes progressively more subdivided towards the edge of the radular row. In particular, there seem to be no reliable radular differences between the Enidae and the Cerastinae. Both Watson and Steenberg, in separating the Cerastinae (= Pachnodinae of Steenberg, 1925) from the Enidae, made much of the distinctly angled disposition of the tooth rows in *Pachnodus*. However this genus is clearly specialised in its dentition, being arboreal, and is not typical of the family as a whole (see for example *Euryptyxis fragosa,* Fig. 19e); such radular modifications to an arboreal mode of life have been shown to be convergent in a number of cerastines (Solem, 1973). The total number of teeth in a row is normally higher in the Cerastinae than in enids and the latter group never approaches the total of 463 teeth recorded by van Mol & Coppois (1980) for *Pachnodus velutinus* Pfeiffer. An analysis of enid tooth number from Hesse's review of the family (Hesse, 1933) shows an average number of 62 (s.d. 17·7; range 29–107) teeth per row.

Crop and Intestinal Folds

Beck (1912: pl. 9, fig. 23.) illustrated the internal structure of the stomach region of *Zebrina detrita* Müller, clearly showing two longitudinal crop folds passing posteriorly to the digestive gland ducts, and two intestinal folds running posteriorly from the ducts to the small intestine. It is evident from Beck's figure that, as in Arabian *Mastus* and *Imparietula*, the intestinal fold emanating from the posterior duct opening is more highly developed than that coming from the anterior duct, and in the Arabian enids it develops into a true flap which extends some distance along the intestine. This is in marked contrast to the cerastines *Euryptyxis* and *Zebrinops* where both intestinal 'folds' are little more than thickenings of the epithelium. The paired crop folds are similarly reduced, and are often barely visible. Such differences are of potential taxonomic significance, but require more-detailed investigation.

Lung cavity

Lung folds are more highly developed in the Cerastinae than in any orthurethran group. A short renal fold is found in some Eninae (Weigmann, 1901; Beck, 1912) and Chrondrulinae

(pers. obs.), as well as certain Pupillidae (Steenberg, 1925), but apparently occurs in all cerastines. Typically it extends the full length of the kidney, and in *Amimopina* (Solem, 1964) and a number of African cerastine genera (pers. obs.) is closed throughout its length, giving rise to the 'pseudosigmurethrous' condition described by Solem (1964); a similar arrangement was also reported for *Acanthinula aculeata* by Watson (1920). In cerastines the renal fold normally joins the rectal fold at the apex of the pallial cavity, the latter then extending downwards to the pneumostome. In juvenile *Euryptyxis* the rectal fold was found to extend down only to the level of the tip of the kidney, but is fully developed in the adult. Rectal folds are found in all Arabian genera, *Pachnodus* (van Mol & Coppois, 1980), *Rachis* (Seshaia, 1932), *Amimopina* (Solem, 1964), as well as *Conulinus, Rhachidina* and *Rhachistia* (pers. obs.). It is known to be lacking only in *Edouardia* (Connolly, 1925; and pers. obs.).

The lung folds of cerastines serve to partition the lung cavity into functionally distinct respiratory and excretory areas, and this is correlated with the development of prominent pallial venation, particularly of the respiratory area. By contrast, no vessels are macroscopically visible on the outer lung wall of enids. Tillier (1982) concluded that in slugs an extensive lung vascularisation increased effective respiratory surface area, and is developed in response to a reduction in lung size. Whilst the cerastine lung is not relatively shorter than in many enids (Table 3), its respiratory area is reduced laterally by the lung folds. Differences in size between the vessels of the lung wall and those within the folds, which are typically narrower, were also noted and may be related to the differing functions of the two areas: the large vessels may, for example, serve to increase the blood supply to resorbtive region of the lung, which would potentially be of great importance in xerophilic taxa. The groove clearly has a resorbtive function in cerastines, as van Mol & Coppois (1980:22) have described a well-developed brush border epithelium in the renal groove of *Pachnodus*.

Reproductive system

Hermaphrodite Duct Diverticulae

These structures were first described from *Ena* and *Zebrina* by Martens & Wiegmann (1898:82), who also pointed out that they were absent from *Pachnodus;* subsequently Wiegmann (1901:282, pl. X, figs 12 & 23) figured similar structures from *Subzebrinus*. Hesse (1933:154) also figured the diverticulae in *Chondrula* and their taxonomic importance was discussed by Steenberg (1925) who referred to them as *culs-de-sac*. They are presented in both Arabian enid species but are absent from the cerastines, and take the form of a clump of blind-ended sacs situated on the hermaphrodite duct between the hermaphrodite gland and the seminal vesicles (Figs 7A, 8B–D, 11A). Their function is unknown although Wiegmann noted that they contained sperm. They are not known from any other Stylommatophora, and appear to form a synapomorphy separating the Enidae from other Orthurethra. Similar-looking structures have been reported in certain Basommatophora by Hubendick (1978) who referred to them as seminal vesicles; whether or not these are homologous with the stylommatophoran seminal vesicles as defined by Bayne (1973) is unknown. What is clear is that the Enidae possess a true seminal vesicle (*sensu* Bayne) in addition to the *culs-de-sac,* suggesting that the latter might be an independent structure formed *de novo*.

Spermoviduct

On the basis of a figure and description in Beck (1912:223, pl. 9, fig. 31), Steenberg (1925) has stated that the enid spermoviduct is differentiated into three grooves; he had earlier described a similar organisation in the Clausiliidae (Steenberg, 1914), and was later to record the presence of this third groove in the Pupillidae (Steenberg, 1929). A similar configuration is found in northern Oman enids. Steenberg referred to this third groove as the 'serous canal' and suggested that it originated from the oviducal portion of the spermoviduct. In cerastines the organisation is different: van Mol & Coppois (1980) described only two grooves in *Pachnodus*, a spermiduct and an oviduct, agreeing with my own histological observations on *Euryptyxis* and *Zebrinops*.

Visser (1977) has recently reviewed the systematic importance of the spermoviduct in the Pulmonata, and although he tentatively included the Clausiliidae in his 'incomplete triaulic'

category, I consider that Steenberg's observations on the clausiliids are better interpreted as the 'semi-diaulic' condition, as the serous canal remains a groove throughout its length, never separating as a free duct. Visser recognised two principal lineages in the Stylommatophora, both containing groups showing the semi-diaulic, monotrematic condition, but apparently differing in the homology of the free male duct (vas deferens). Group A, where the vas deferens forms from the sperm groove, included the Clausiliidae (the 'serous canal' is presumably equivalent to Visser's 'seminal groove' which serves to transport exogenous sperm). Group B incorporates some Pacific Orthurethra (Achatinellidae) and the Succineidae and is characterised by a vas deferens originating from the seminal groove.

Although both the Enidae and the Cerastinae are at Visser's semidiaulic level of organisation and would appear to fall within the stylommatophoran group A, they clearly differ fundamentally by the presence of a third spermoviducal canal in the former. Visser (1977:48) admits that 'two morphologically widely divergent types of reproductive system as displayed by (i) *Achatina* and (ii) *Agriolimax*' are included under the semi-diaulic designation in group A. The differences between the spermoviducts of enids and cerastines are analogous with those of Visser's examples: *Achatina* with a spermoviduct 'consisting of a female channel, a sperm groove and a seminal groove', and *Agriolimax* where 'the spermoviduct consists solely of a female channel and the sperm groove'.

Terminal Genitalia
It is generally recognised that the terminal genitalia of land molluscs provide a rich source of taxonomically important information below the family level (Solem, 1978), and Cain (1982) referred specifically to gastropod genitalia in exemplifying what he termed 'privileged characters' in a taxonomic sense.

Some useful family-level characteristics also are to be found in the terminal region, particularly in the Cerastinae where the overall pattern appears to be remarkably constant. A highly characteristic brown spongy tissue is found lining the atrium and vagina of most cerastines. This was first noted by Seshaiya (1932) in *Rachis,* but is also present in *Amimopina* (Solem, 1964), *Pachnodus* (van Mol & Coppois, 1980), *Euryptyxis, Cerastus, Zebrinops, Acatinelloides, Edouardia, Rachistia,* and probably most other members of the subfamily; the only group for which it has been noted as absent is in central African *Cerastus* (Verdcourt, 1970). The histology has been described by van Mol & Coppois (1980), who noted the presence of melanin and elastic fibres in the cells, and similar tissue has not been described in any other group. Additionally, a spermatheca lacking a diverticulum is always developed, and typically joins the free oviduct close to or at the commencement of the melanic tissue.

Of particular interest within the Orthurethra is the development of a penial appendix. An appendix with a remarkably uniform basic structure is found in many pupillacean groups in addition to the Enidae and Cerastinae: the Achatinellidae, Orculidae, Cionellidae, Amastridae, Pupillidae, Vertiginidae and Valloniidae. It seems probable that it is homologous within these various groups, and its presence defines Shilieko's suborder Pupillina (Shileiko, 1979).

At lower taxonomic levels too, the anatomy of the penial appendix provides valuable information. It is broadly separable into three regions; a relatively short basal portion which internally bears pilasters, and which may be everted (Figs 11C, 37A); a long, thin central stalk which is thick-walled and has only a very narrow lumen; and an elongate, apical sac which is thin walled with a large lumen. Shilieko (1979, fig. 4) recognised a total of five regions by including areas of differentiation at the top of the basal portion, and at the base of the central stalk. The function of the penial appendix is unknown, although Shileiko (1979) suggested it might act as a receptacle for autosperm prior to its injection into the spermatophore, and Forcart (1940) that it acted as a mechanical stimulator. It is present in all cerastines. The region of transition between the basal and central portions of the appendix, where the retractor muscle inserts, has proved to be of considerable taxonomic value in the cerastines, particularly at the generic level. In Arabian *Euryptyxis* the muscle inserts more-or-less directly at the junction, although it may expand and embrace the base of the central stalk just prior to attachment. In *Zebrinops* (Fig. 37D), and to a

greater extent in *Cerastus* (Fig. 15A), the muscle actually encloses the stalk base, becoming attached at the top and forming an enclosed lumen; this trend is even more pronounced in the Ethiopian and Somali species of *Cerastus* and *Zebrinops* (Mordan, pers. obs.). The enclosure of the base of the central stalk is accompanied by the projection of the tip of the stalk into the basal lumen as an elongate papilla, which is particularly prominent in *Zebrinops* (Fig. 37D). The degree of contraction of the muscular sheath would partly determine the extent of protrusion of the papilla, and this may in turn be related to the state of relaxation of the individual specimen. Nevertheless, real differences in the length of the sheath, and of the papilla, do appear to exist between taxa.

The penis has a muscular sheath which is attached only at its top, and which in certain species appears always to be reflected to form a double-layered structure. There is a clearly demarked caecum which varies greatly in both size and shape between species, ranging from a short bulb in *Euryptyxis* to a long, so-called 'flagellum' in *Cerastus*. Whilst there are marked differences in both pilaster pattern and degree of differentiation of the caecal area between genera, within *Euryptyxis*, for example, pilaster pattern is fairly uniform: paired glandular pads embrace the epiphallar pore and extend downwards as pilasters which may bifurcate. Normally there is a further pair of glandular pads and associated pilasters opposite the pore. In two of the four species of *Euryptyxis* the glandular pads are divided latitudinally by a groove running round the penis below the level of the pore (Figs 24B, 27B), but in *E. candida* and *E. latireflexa* (Figs 21C, 31C) the groove appears to be absent. This groove is also well defined in *Zebrinops*, but in this genus no large glandular pads extend above it and the whole area of the caecum is dotted with small glandular areas (Fig. 37D).

The epiphallus itself has a relatively simple structure in *Euryptyxis* and *Zebrinops*, and appears externally as a thickened portion of the vas deferens with a series of transverse ridges or folds corresponding to a single internal row of pits which mould the spines of the spermatophore. The number of these pits does vary within species, but in the case of the four recognised Arabian species of *Euryptyxis* at least, there is no overlap in range between individual species (Table 5). An analysis of variance of the data shows highly significant between-species variation ($F = 168 \cdot 53$, d.f. 3,31. $p < 0 \cdot 001$). The African species *E. revoili* (24-25 pits) falls within the range of the Arabian *E. latireflexa* (17-28 pits), but the geographical distributions of these two species do not overlap. Moreover, their terminal genitalia differ in a number of other significant respects. Although most of the data in Table 5 were obtained from sympatric populations, where interspecific differences might be expected to be more pronounced, the limited evidence from allopatric populations of *E. fragosa* and *E. latireflexa* suggests this is not the case. Much larger epiphallar differences existed between syntopic *E. fragosa* and *E. candida* at Taizz, than between *latireflexa* and *labiosa* in Dhofar, but whereas the latter species pair differ in size quite markedly, the former are of very similar adult size and some alternative species-isolation mechanism such as genital or spermatophore incompatibility might need to be invoked.

The spermatophore of *Euryptyxis* is unknown except for a few broken fragments found in the spermatheca of *E. fragosa*. These suggest that the structure is similar to *Zebrinops*, but at least some of the spines have five points at their tip rather than two as in *Z. albata*. *Cerastus schweinfurthi* also has a single row of spines on the spermatophore. It is tempting to speculate on the possibility of the spermatophore structure acting as, or reinforcing, some form of species-isolation mechanism, but direct evidence is lacking, and the importance of inter-specific genital differences in mechanical isolation may well have been overestimated (Mayr, 1963). Nevertheless, such characters can be of considerable empirical value in taxonomy (Arnold, 1973, 1983), and although the epiphallus cannot be considered a part of the external genitalia, it does secrete the spermatophore and presumably would be subject to selection pressures similar to those acting on the external genital organs.

The Enidae exhibit a rather greater variety of terminal genital structures than do the cerastines. In particular, the penial appendix is lacking in a number of genera, and a diverticulum is often developed on the spermathecal stalk. Forcart (1940) based his separation or the Turkish Enidae into the two subfamilies Eninae and Chondrulinae on the presence or absence of the penial appendix, and on this basis both subfamilies are represented in northern Oman. The generic

placement of the two northern Oman enids is based principally on the anatomy of the terminal genitalia.

Ecology

Extremely little is known of the ecology of the southern Arabian land snail fauna. In common with most desert pulmonates much of the year is spent in aestivation, with only limited periods of activity during the wet seasons. The main precipitation results from the south-west monsoon during July and August, but there may be other shorter periods of rainfall during the year. In general, cerastines aestivate in shaded situations on trees and rocks, normally some distance above ground level. *Mastus* and *Imparietula* are known to utilise similar sites, but they are also commonly found in considerable numbers in soil under rocks and ground litter such as palm fronds. Whilst most cerastine species are largely restricted to upland regions, *Imparietula* and *Mastus* also occupy synanthropic sites in plantations and near houses at lower elevations.

A consideration of population structure of *Euryptyxis* during aestivation suggests that in most species maturity is normally reached in two growing seasons (not necessarily annual), and that the adults subsequently live for a number of years. Only two size classes appear to be represented, and adults greatly outnumber the juveniles.

The importance of predation is uncertain, but many aestivating colonies of *Euryptyxis* in Dhofar showed evidence of some snails having been broken off, leaving the shell lip adhering to the substrate. The most likely predators are small mammals such as the spiny mouse *Acomys*, three species of which are recorded from Dhofar (Harrison, 1980), and the rat *(Rattus rattus)* which is now present in many areas. Rodents in particular are known to exert a significant effect on population densities of desert snails in the Negev (Yom-Tov, 1970).

Sympatry of closely related species is of considerable taxonomic interest as it can provide the only situations in which the species may interact. In the problematical genus *Euryptyxis* the syntopic occurrence of the following species pairs was recorded: *E. fragosa* and *E. candida* [Taizz, 1978-79]; and *E. latireflexa* and *E. labiosa* [Tawi Atair, 1977-78]. It also seems likely that *Cerastus schweinfurthi* and *C. scotti* co-occur at Jebel Harir (Connolly, 1941), but living material is lacking. From the limited information available, however, there was no real evidence for any form of character displacement in sympatric populations when compared with those from allopatric situations.

Summary and conclusions

A total of sixteen species of Enidae *sensu lato* are recognised in the present revision, from a list of thirty nominal species given by Connolly (1941); only one, *Cerastus albonotata* Verdcourt, has been newly described since that time. Whilst these figures appear to represent a synonymy ratio of 2:1, such a conclusion would be false, as almost the entire synonymy is accounted for within the single genus *Euryptyxis*.

The most significant taxonomic changes presented concern the generic repositioning of a number of taxa listed by Connolly under *Euryptyxis,* and in particular the placement of the northern Oman species into genera belonging to the essentially Palaearctic subfamilies Eninae and Chondrulinae. Within the Cerastinae, the existing generic units have been retained, but have now been defined in terms of anatomical as well as shell characters. In doing this it has been necessary to use additional corroborative data on closely related taxa from Somalia, Ethiopia and Socotra. In general there has been insufficient material to assess anatomical variation adequately. Indeed the anatomy of a large number of the taxa remains unknown. The greatest information was available for the commonest and most-widespread genus *Euryptyxis* and here in was demonstrated that species were better defined in terms of epiphallar rather than penial anatomy, suggesting that spermatophore morphology might play a role in species isolation.

Consistent, and I believe significant, anatomical differences have been shown to exist between the northern subfamilies Eninae and Chondrulinae (referred to here as the Enidae *sensu stricto),*

and the southern Cerastinae. The former are uniquely defined by the possession of a clump of *culs-de-sac* on the hermaphrodite duct, whilst the latter show a number of specialisations of the pallial complex, apparently related to water conservation, as well as of the reproductive system. Moreover, there appear to be no synapomorphic characters to unite the two as sister groups in a cladistic sense. Formalization of these differences in nomenclature is, however, deferred until there is greater knowledge of the anatomy of related orthurethran families.

Acknowledgements

References

Albers, J. C. 1860. *Die Heliceen nach naturlicher Verwandtschaft systematisch geordnet.* Second Edition. 359pp. Leipzig: Engelmann.

Ancey, C. F. 1906. Relevé des mollusques terrestres et fluviatiles de la Pénsule Arabique. *J. Conch. Paris* **53**: 257–271.

Arnold, E. N. 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides and Psammodromus* (Reptilia:Lacertidae). *Bull. Br. Mus. nat. Hist.* (Zool). **25**: 291–366.

—— 1983. Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia:Lacertidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **44**: 291–339.

Bayne, C. J. 1973. Physiology of the pulmonate reproductive tract: location of spermatozoa in isolated, self-fertilising succineid snails (with a discussion of pulmonate tract terminology). *Veliger* **16**: 169–175.

Beck, H. 1837. *Index Molluscorum.* 124pp. Hafniae.

Beck, K. 1912. Anatomie deutscher Buliminus-Arten. *Jena. Z. Naturw.* **48** (2): 187–262.

Bourguignat, M. J. R. 1857. Améneties malacologiques. *Revue Mag. Zool.* Ser. 2, **9**: 3–21.

—— 1876. *Species novissimae Molluscorum in Europaeo systemati delectae* . . . 80pp. Lutetiae.

—— 1882. *Mission G. Révoil au Pays Comalis. Mollusques Terrestres et Fruviatiles.* 108pp. Paris.

Bruguière, J. G. 1792. *Encyclopédie Méthodique, Histoire Naturelle des Vers.* **1** 757pp. Paris.

Cain, A. J. 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Phil. Trans. R. Soc., B.* **27** (956): 377–428.

—— 1981. Possible ecological significance in shape of *Cerion* shells with age. *J. Conch. Lond.* **30**: 305–315.

—— 1982. On homology and convergence. *In* K. A. Joysey & A. E. Friday, *Problems of phylogenetic reconstruction. The Systematics Association Special Volume* **21**: 1–19.

—— 1983. Ecology and ecogenetics of terrestrial molluscan populations. *In:* K. M. Wilbur (Ed.), *The Mollusca* **6**: 597–647. Academic Press. London & New York.

Connolly, M. 1925. The non-marine Mollusca of Portugese East Africa. *Trans. R. Soc. S. Afr.* **12** (3): 105–220.

—— 1941. South Arabian non-marine Mollusca. *Expedition to south-west Arabia, 1937–8.* **1** (4): 17–42.

Dance, S. P. 1966. *Shell Collecting. An Illustrated History.* 344pp. Faber & Faber, London.

Dejean, Baron. 1821. *Catalogue de la collection des Coléoptères.* 136pp. Paris.

Delessert, B. 1841. *Recueil de coquilles décrites par Lamarck* . . . 40 Pls. Paris.

Dillwyn, L. W. 1817. *A descriptive catalogue of recent shells, arranged according to the Linnaean method; with particular attention to the synonymy.* 1092pp. London.

Férussac, J. B. L. A. de. 1821–22. *Tableau systématiques des animaux mollusques* 114pp. Paris.

—— 1827. *Bull. Sci. nat. Geol.* **8**: 85.

Férussac, J. B. L. A. de. & Deshayes, G. P. 1951. Histoire naturelle générale et particulière des Mollusques. . . . 2 Vols., Atlas. Paris.

Fischer-Piette, E. & Métivier, B. 1972. Sur quelques mollusques terrestres du sud-est de l'Arabie. *Bull. Mus. Hist. nat. Paris* 3e série. **93**: 1289–1310.

Forcart, L. 1940. Monographie der Türkischen Enidae (Moll., Pulm). *Verh. naturf. Ges. Basel* **51** (1): 106–364.

Forskal, P. 1775. *Descriptiones Animalium*. 140pp. Hauniae.

Gmelin, J. F. 1791. *Linnaeus, Sysema Naturae*, 13th Ed. **I** (6): 3021–3909. Lipsiae.

Gittenberger, E. 1967. Die Enidae (Gastropoda, Pulmonata) gesammelt von der Neiderländischen biologischen Expedition in die Türkei in 1959. *Zool. Meded. Leiden* **42** (13): 125–141.

Harrison, D. L. 1980. The mammals obtained in Dhofar by the 1977 Oman Flora and Fauna Survey. *Journal of Oman Studies, Special Report* **2**: 387–397.

Heller, J. 1971. Revision of the genus *Paramastus* Hesse (Enidae). *Arch. Molluskenk.* **101** (5–6): 263–273.

——— 1974. Systematics and distribution of the land snail *Pene* (Pulmonata: Enidae) in Israel. *Zool. J. Linn. Soc.* **54** (4): 257–276.

——— 1975. The taxonomy, distribution and faunal succession of *Buliminus* (Pulmonata: Enidae). *Zool. J. Linn. Soc.* **57** (1): 1–57.

Herrmannsen, A. N. 1847. *Indicis generum malacozoorum primordia . . .* **2**: 1–352. Casselis.

Hesse, P. 1933. Zur Anatomie und Systematik der Familie Enidae. *Archiv Naturgesch.* N.F. **2** (2): 145–224.

Hubendick, B. 1978. Systematics and comparative morphology of the Basommatophora. *In:* V. Fretter & J. F. Peake (Eds.), *Pulmonates* **2A**: 1–47.

Jousseaume, F. 1889. Espèces nouvelles des environs d'Aden suivies d'un apercu sur la faune malacologique de la Péninsule Arabique. *Bull. Soc. malac. Fr.* **6**: 345–362.

——— 1890. Espèces terrestres de Massaouah, de Perim et d'Aden. *Bull. Soc. malac. Fr.* **7**: 81–102.

——— 1894. Diagnose des coquilles de nouveaux mollusques. *Bull. Soc. philomath. Paris. 3rd Series* **6** (3): 98–104.

——— 1899. Description of coquilles nouvelles. *Naturaliste* 2nd. Series **13**: 8.

Kobelt, W. 1902. Die Familie Buliminidae. In *Systematisches Conchilien-Cabinet*. pp. 397–1051. Nurnberg.

Küster, H. C. & Pfeiffer, L. 1845–55. Die gattung *Bulimus*. In: *Systematisches Conchilien-Cabinet*. 395pp. Nurnberg.

Lamarck, J. P. B. A. de M. de 1822. *Histoire Naturelle des Animaux sans Vertèbres*. **6** (2) 232pp. Paris.

Lindholm, W. A. 1925. Beitrage zur Systematik und Nomenklatur der Familie Enidae (Buliminidae). *Arch. Molluskenk.* **57**: 23–41.

Martens, E. von, 1895. Neuen *Buliminus* aus Süd-Arabien. *Sber. Ges. naturf. Freunde Berl.* 1895 (6): 129–130.

Martens, E. von & Wiegmann, F. 1898. Land- und Süsswasser-Mollusken der Seychellen. *Mitt. zool. Samml. Mus. Naturk. Berl.* **1** (1): 1–94.

Martini, F. H. W. & Chemnitz, J. H. 1786. *Neues systematisches Conchylien-Cabinet*. 9 345pp., 33 pls. Nuremberg.

Mayr, E. 1963. *Animal species and evolution* 797pp. Cambridge, Mass.

Melvill, J. C. 1894. Descriptions of two new species of terrestrial Mollusca from the Hadramaut District, South Arabia. *Proc. malac. Soc. Lond.,* **1**: 224–225.

Mermod, G. 1951. Les types de la collection Lamarck au Muséum de Genève. Mollusques vivants II. *Revue suisse Zool.,* **58** (40): 693–753.

Mol. J.-J. van, & Coppois, G. 1980. Mollusques, Enidae. *Revue zool. afr.* **94**: 15–60.

Mordan, P. B. 1980*a*. Molluscs of Saudi Arabia: land molluscs. *Fauna of Saudi Arabia* **2**: 359–367.

——— 1980*b*. Land Mollusca of Dhofar. *Journal of Oman Studies* Special Report. **2**: 103–111.

——— 1984. Taxonomy and biogeography of southern Arabian Enidae (sensu lato) (Pulmonata:Pupillacea). *In:* A. Solem & A. C. van Bruggen (Eds) *World-wide Snails: Biogeographical studies on non-marine Mollusca*. 289pp. Leiden.

Müller, O. F. 1774. *Vermium terrestrium et fluviatilum . . .* Vol. II, Havniae & Lipsiae.

Paladilhe, A. 1872. Voyage de Mrs. Antinori, Beccari et Issel dans la Mer Rouge et la pays des Bogos. Mollusques. II. Description de quelques espèces nouvelles des environs d'Aden. *Annali Mus. civ. Stor. nat. Genova* **3**: 12–26.

Pallary, P. 1925. Note on some terrestrial Mollusca from the hinterland of Makalla. *In:* O. H. Little (Ed.) *The geography and geology of Makalla (South Arabia)*. 223–234. Cairo.

——— 1928. Mollusques continentaux du Sud de l'Arabie collectés en 1926 par M. Lees. *Proc. malac. Soc. Lond.* **18**: 39–42.

Peake, J. F. 1978. Distribution and ecology of the Stylommatophora. *In:* V. Fretter & J. F. Peake (Eds) *Pulmonates* **2A**: 429–526.

Pfeiffer, L. 1842. *Symbolae ad Historiam Helicorum*. II. 1–147. Cassel.

—— 1858. Diagnosen neuer Schnecken-Arten. *Malakozool. Bl.* **5:** 238–240.

Pilsbry, H. A. 1897. New Lower Californian Bulimuli. *Nautilus* **10:** 102–3.

—— 1897–98. *Manual of Conchology.* Second series: Pulmonata. Vol XI. 339pp. Philadelphia.

Pilsbry, H. A. & Cooke, C. M. 1914. *Manual of Conchology.* Second series: Pulmonata. Vol XXII. 428pp. Philadelphia: Academy of Natural Sciences.

Pollard, E. 1975. Differences in shell thickness in adult *Helix pomatia* from a number of localities in southern England. *Oecologia* **21:** 85–92.

Récluz, C. A. 1843*a*. Description de coquilles rapportées par M. Jehenne. *Revue zool.* **1843** (1): 2–5.

—— 1843*b. Magasin Zool.* Paris Series 2, Classe 5, 5: pls. 75–76. Paris.

Reeve, L. A. 1849. Monograph of the genus *Bulimus. In Conchologica Iconica* 5. 89pls. London.

Rossmassler, E. A. 1835–1920. *Iconographie der Land- & Süsswasser Mollusken . . .* Series 1 and 2. Completed P. Hesse. Dresden, Leipzig, & Berlin.

Selander, R. K. & Hudson, R. O. 1976. Animal population structure under close inbreeding: the land snail *Rumina* in southern France. *Am. Nat.* **110:** 695–718.

Seshaiya, R. V. 1932. Anatomy of *Rachisellus punctatus* (Anton). *Annamalai University Journal* **1** (1): 72–90.

Shachak, M., Orr, Y. & Steinburger, Y. 1975. Field observations on the natural history of *Sphincterochila (S.) zonata* (Bourguignat, 1853). *Argamon* **5** (1–4): 20–46.

Shileiko, A. A. 1979. The system of the order Geophilla (= Helicida) (Gastropoda Pulmonata). *Proceedings of the Zoological Institute, Academy of sciences of the USSR.* **80:** 44–69.

Smith, E. A. 1894. On a small collection of land and freshwater shells from Oman, Arabia. *Proc. malac. Soc. Lond.* **4** (4): 141–142.

—— 1903. Land and freshwater shells of Socotra and Abdel-Kuri. *Liverpool Museum Reports, Socotra Expedition.* pp. 111–158.

Smythe, K. & Gallagher, M. 1977. Land and freshwater Mollusca. *Journal of Oman Studies* Special Report. **1:** 219–225.

Solem, A. 1962. Notes on, and descriptions of New Hebridean land snails. *Bull. Br. Mus. nat. Hist.* (Zool.) **9** (5): 217–247.

—— 1964. *Amimopina,* an Australian enid land snail. *Veliger* **6** (3): 115–120.

—— 1973. Convergence in pulmonate radulae. *Veliger* **15** (3): 165–171.

—— 1978. Classification of the land Mollusca. *In:* V. Fretter & J. F. Peake (Eds), *Pulmonates* **2A:** 49–97. London.

—— 1979. Biogeographic significance of land snails, Paleozoic to Recent. *In:* J. Gray & A. J. Bucot (Eds) *Historical biogeography, plate tectonics and the changing environment.* pp. 277–287. Oregon.

Steenberg, C. M. 1914. Anatomie des Clausilies Danoises. I. Les organes génitaux. *Mindeskrift for Japetus Steenstrup* **29:** 1–44.

—— 1925. *Etudes sur l'Anatomie et la Systématique des Maillots.* 211pp., 34 pls. Copenhagen.

—— 1929. Recherches sur l'anatomie et la place systématique du genre *Agardhia* Gude (Gastropoda Pulmonata, fam. Pupillidae *s. lat.*). *Vidensk. Meddr. dansk naturh. Foren.* **88:** 15–29.

Sykes, E. R. 1902. Description of *Cerastus dinshawi* n. sp. from Aden with a note on *Otopoma. Proc. malac. Soc. Lond.* **5:** 338–9.

Taha, M. F., Harb, S. A., Nagib, M. K. & Tantawi, A. H. 1981. The climate of the Near East. *In:* K. Ttakahashi & H. Arakawa (Eds), *World survey of climatology.* 333pp. Amsterdam.

Tillier, S. 1981. Clines, convergence and character displacement in New Caledonian diplommatinids (Land Prosobranchs). *Malacologia* **21** (1/2): 177–208.

—— 1982. Structures respiratoires et excrétrices des limaces (Gastropoda:Pulmonata:Stylommatophora). *Bull. Soc. Zool. Fr.,* **108:** 9–19.

Verdcourt, B. 1966. Notes on the genus *Conulinus* MARTENS (Enidae). *Arch. Molluskenk.* **95** (5/6): 279–286.

—— 1970. The genus *Cerastua* Strand (Mollusca-Enidae) in the Congo Republic, Burundi and Rwanda. *Revue zool. afr.* **82** (1–2): 14–34.

—— 1974. Notes on a small collection of non-marine Mollusca from Yemen. *J. Conch. Paris* **111:** 3–8.

Visser, M. H. C. 1977. The morphology and significance of the spermoviduct and prostate in the evolution of the reproductive system of Pulmonata. *Zoologica Scr.* **6:** 43–54.

Watson, H. 1920. The affinities of *Pyramidula, Acanthinula,* and *Vallonia. Proc. malac. Soc. Lond.* **14** (1): 6–30.

Wenz, W. 1923. Gastropoda extramarina tertiaria II, Pulmonata II. *In:* J. F. Pompeckj, *Fossilium Catalogus.* p. 885–1734. Junk: Berlin.

Westerlund, C. A. 1887. *Fauna der in der Paläartischen Region Lebenden Binnenconchylien.* **1** (3). 183pp. Lund.

Wiegmann, F. 1901. Binnen-Mollusken aus Westchina und Centralasien. II. Die Buliminiden. *Ezheg. zool. Muz.* **6:** 221–298.

Woodruff, D. S. 1978. Evolution and adaptive radiation of *Cerion:* a remarkably diverse group of West Indian land snails. *Malacologia* **17:** 223–239.

Yom-Tov, Y. 1970. The effects of predation on population densities of some desert snails. *Ecology.* **51:** 907–911.

Zilch, A. 1951. Ergebnisse zoologisch-geologischer Sammelreissen H. Kaltenbach's in NO-Afrika, 5: Familie Enidae. *Arch. Molluskenk.* **80:** 33–46.

—— 1959. Gastropoda 2. Euthyneura. *In:* O. H. Schindewolf (Ed.), *Handbuch der Paläozoologie.* pp 1–200. Berlin. PA

Abbreviations used in figures

A	anus		MG	mantle gland
AC	albumen chamber		MS	muscle sheath
AD	albumen duct			
AG	albumen gland		O	oviduct
AO	aorta		OE	oesophagus
AP	appendicular papilla			
AR	appendicular retractor		P	penis
AT	atrium		PA	penial appendix
ATR	atrial retractor muscle		PI	pilaster
AU	auricle		PP	penis papilla
			PR	penis retractor
C	caecum		PN	pneumostome
CR	crop		PV	pulmonary vein
E	epiphallus		R	rectum
EC	epiphallar caecum		RNF	renal fold
EF	epiphallar flagellum		RTF	rectal fold
EP	epiphallar pore		RO	renal orifice
EPT	epiphallar pit			
			S	spermatheca
I	intestine		SD	spermathecal diverticulum
			SG	salivary gland
GO	genital orifice		SO	spermoviduct
			ST	stomach
HD	hermaphrodite duct		SV	seminal vesicle
HDC	hermaphrodite duct culs-de-sac			
HG	hermaphrodite gland		T	talon
K	kidney		V	vagina
			VD	vas deferens
MC	mantle collar		VE	ventricle

Manuscript accepted for publication 29 October 1985